

# THE BASES OF ANGIOSPERM PHYLOGENY: PALYNOLOGY<sup>1,2</sup>

JAMES W. WALKER<sup>3</sup> AND JAMES A. DOYLE<sup>4</sup>

## ABSTRACT

The field of palynology is reviewed in terms of its contributions to angiosperm systematics and phylogeny. Principal pollen characters which are phylogenetically useful at higher taxonomic levels (including aperture type, pollen wall architecture, pollen-unit, polarity, symmetry, shape, and grain size), and their evolutionary trends are examined. Many palynological characters and concepts are subjected to re-examination, particularly in an evolutionary-phylogenetic context. An attempt is made to show how pollen characters correlate with various higher categories of the Takhtajan and Cronquist systems of angiosperm classification and to outline certain phylogenetic trends observed in the pollen of different groups of angiosperms. With some exceptions, pollen morphology is consistent with the levels of relative advancement and the relationships postulated in the Takhtajan and Cronquist systems. Angiosperm pollen grains are clearly divisible into two fundamentally different types (each with its own derivatives): heteropolar, bilateral, boat-shaped *monosulcate* pollen versus isopolar, radio-symmetric, globose *tricolpate* pollen. "Gymnospermous" monosulcate pollen and derivative types (ulcerate, disulculate, etc.) characterize both the putatively primitive dicotyledonous subclass Magnoliidae and the monocotyledons. The six non-magnoliid dicotyledonous subclasses, on the other hand, are characterized by tricolpate pollen and derivative types (tricolporate, triporate, rugate, etc.). Relatively primitive tricolpate pollen is retained by many Ranunculidae,

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<sup>2</sup> The general introduction, principal phylogenetically useful pollen characters, comparative palynology of the subclass Magnoliidae, palynological technique, and major palynological reference works sections were prepared by J. W. Walker. The section on comparative palynology and the Takhtajan and Cronquist systems of angiosperm classification (exclusive of the subclass Magnoliidae) and the general summary and conclusions were prepared by J. A. Doyle.

<sup>3</sup> Department of Botany, University of Massachusetts, Amherst, Massachusetts 01002.

<sup>4</sup> Department of Botany and Museum of Paleontology, University of Michigan, Ann Arbor, Michigan 48104.



Caryophyllidae, and "lower" Hamamelididae. The Dilleniidae (except Dilleniaceae) and Rosidae are somewhat more advanced in having basically compound-aperturate tricolporate pollen. The subclass Asteridae, which retains indications of a rosoid ancestry, exhibits the greatest array of specialized pollen types. The most important palynological contradiction of the Takhtajan and Cronquist systems is the fact that the highly specialized, basically triporate pollen of the "higher" Hamamelididae (Amentiferae) can be more directly related to triangular tricolporate pollen of the Rosidae than to the tricolpate pollen of the "lower" Hamamelididae. Briefer sections of the paper deal with pollen technique and the major reference works of systematic palynology.

Palynology (from the Greek words, to strew or sprinkle, fine meal; cognate with the Latin *pollen*, flour or dust) is the study of pollen and spores. Although paleontologists have extended its coverage to include organisms or parts of organisms that fall in the spore-pollen size range, such as coccolithophorids, dinoflagellates, diatoms, desmids, hystrichosphaerids, fungal elements, microforaminifera, radiolaria, etc., this paper is restricted to consideration of pollen of flowering plants, even though what is said may be related sometimes to the pollen of gymnosperms or even to pteridophyte spores. Among the bases of angiosperm phylogeny, palynology is unique in that through no other study can one obtain as great an amount of information from so little material in such short a time. Indeed, few fields of botanical inquiry permit as many specimens to be prepared and their variation observed as rapidly as the study of pollen morphology (cf. Van Campo, 1966).

The purpose of this paper is two-fold. First, principal pollen characters which are phylogenetically useful and their major evolutionary trends are examined. In this section many palynological characters and concepts are subjected to re-examination, particularly in the context of phylogeny and evolution. Secondly, an attempt is made to show how these pollen characters correlate with various higher categories in the Takhtajan (1969) and Cronquist (1968) systems of angiosperm classification and to outline certain phylogenetic trends observed in the pollen of different groups of angiosperms. Briefer sections treat palynological technique in general and major palynological reference works.

#### PRINCIPAL PHYLOGENETICALLY USEFUL POLLEN CHARACTERS

Principal phylogenetically useful pollen characters and their evolutionary trends are discussed in this section. Pollen characters which are only of limited taxonomic importance at the generic level or lower are largely ignored. Since systematic palynology is a relatively recent science, frequently less consensus of opinion has been reached in the development and application of its terminology than is the case with other areas of botany. Where it appeared necessary, new palynological terms and definitions have been adopted and certain concepts clarified. In all such cases a guiding principle has been to preserve terminology and definitions which are in wide usage as much as possible; however, in some instances, changes in terminology, definitions, or concepts were felt warranted either because new data have become available (particularly from scanning electronmicroscopy combined with study of thin-sections of the pollen wall) or because use of certain pollen characters in a phylogenetic context made a more evolutionary set of terms imperative. Pollen characters have been grouped into



seven categories, which will be treated in the following order: aperture type, pollen wall architecture, pollen-unit, polarity, symmetry, shape, and grain size.

#### POLLEN APERTURES

Apertures are specially delimited, generally thin-walled areas in the outer pollen wall or exine through which the pollen tube usually (but not always) emerges at the time of germination. Although most apertures seem to represent thinner areas in the exine or aperture membranes, in some pollen grains they are as thick or thicker than the exine on nonapertural areas of the same grain. Thus, it appears that the primary prerequisite for an aperture involved in pollen tube exitus is not so much a thinning of the exine, as development of a zone that is thinner or thicker, as compared with the rest of the pollen wall, which may act as a weak point of rupture during germination of the pollen grain. Apertures serve a second major function in that they allow for volume-change accommodations (harmomegathy) in pollen grains subjected to changes in humidity (Wodehouse, 1935; Payne, 1972). Some apertures may serve both for pollen tube exitus and harmomegathic changes, while some pollen grains have "pseudo-apertures" which appear to function solely in a harmomegathic capacity.

Numerous terms exist to describe pollen apertures. Although some of these have been proposed in papers dealing with the pollen morphology of a limited taxonomic group, such as a family, genus, etc., most aperture terms commonly in use today have been taken either from Erdtman (Erdtman, 1966; Erdtman & Vishnu-Mittre, 1956; Erdtman & Straka, 1961) or Faegri & Iversen (1964). While the aperture terminology developed by Faegri and Iversen has the advantage of simplicity, that developed by Erdtman (which has been frequently modified or changed) is more useful phylogenetically. The description of aperture types outlined in this paper is based largely on the earlier aperture terminology developed by Erdtman, although certain novelties have been introduced.

Pollen apertures may be categorized largely on the basis of their (1) number, (2) shape, (3) position, and (4) structure (i.e., whether they are simple or compound). For routine pollen identification, aperture number, shape, and structure are often all that is required. However, in a phylogenetic-evolutionary context, *position* of the aperture(s) is of paramount importance.

*Aperture Number.*—With respect to number of apertures, pollen appears to be best classified phylogenetically as: (1) inaperturate (without any apertures), (2) mono-aperturate (with one aperture), (3) di-aperturate (with two apertures), (4) tri-aperturate (with three apertures), or (5) poly-aperturate (with more than three apertures). Poly-aperturate pollen grains are most frequently tetra-, penta-, or hexa-aperturate (i.e., with 4, 5, or 6 apertures).

*Aperture Shape.*—With regard to shape (and irrespective of position), pollen grains basically may have three different types of apertures, including: (1) elongate, furrow-like apertures (colpate pollen, sensu lato), (2) round, pore-like apertures (porate pollen, sensu lato), and (3) encircling, ring- or band-like apertures (zonate pollen). Weakly defined apertures may be indicated by introduction of the syllable -oid- into the terms describing the corresponding well-developed apertures, e.g., colpoidate pollen would have poorly developed furrow-



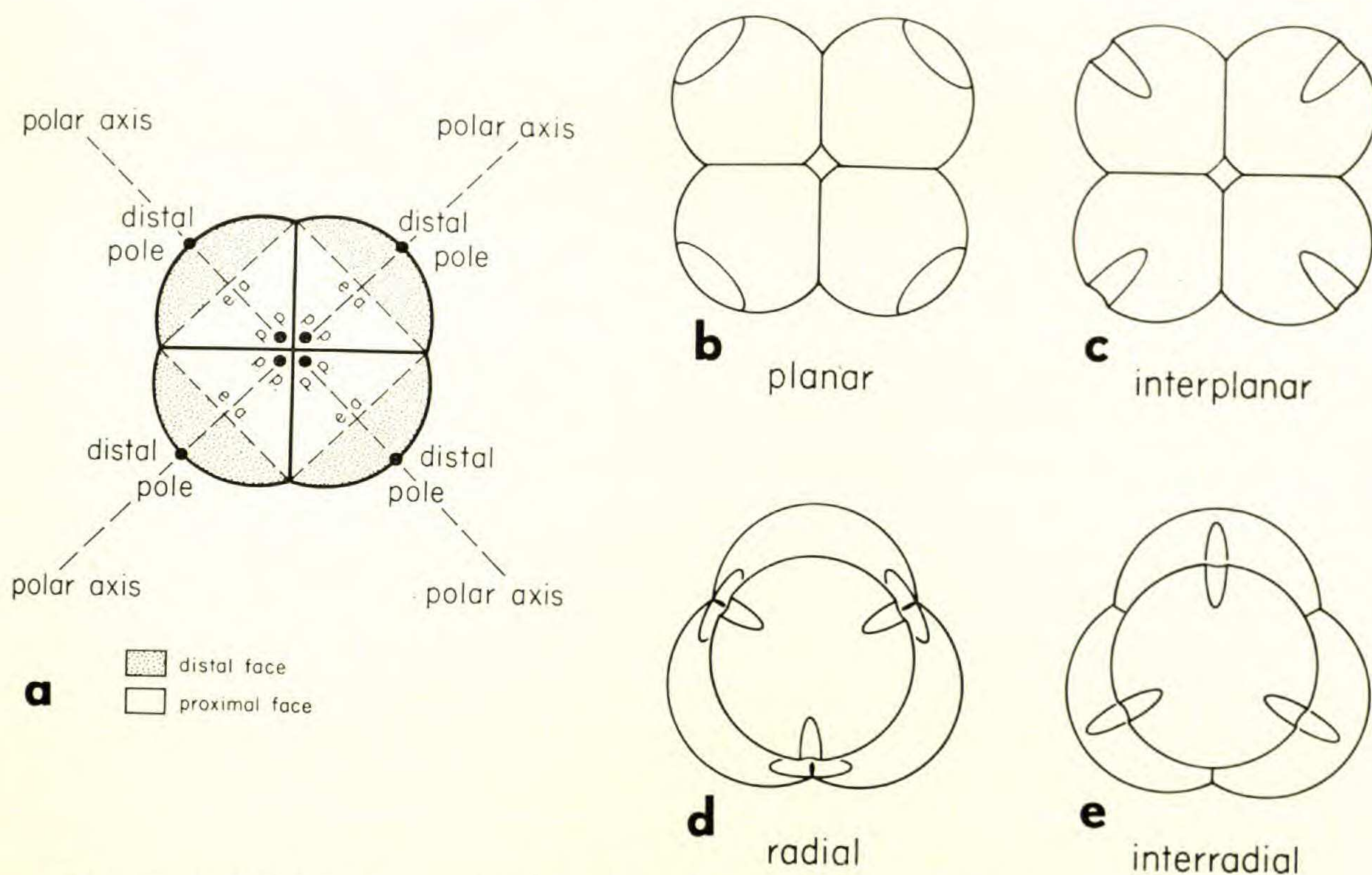


FIGURE 1. Relationships of pollen tetrads and aperture positions.—a. Diagram of a tetragonal pollen tetrad showing the polar axis, one equatorial axis (e.a.) of the equatorial plane, the distal face, the proximal face, the distal pole, and the proximal pole (p.p.) of each pollen grain in the tetrad.—b–c. Tetragonal tetrads showing placement of distal-polar, furrow-like apertures in planar and interplanar positions.—d–e. Tetrahedral tetrads showing placement of equatorial, furrow-like apertures in radial and interradiar positions; top pollen grain shown in polar view with its polar axis perpendicular to the plane of the figure.

like apertures or colpoids. Pollen with one or more weakly defined, more or less irregularly shaped aperturoid areas may be described as tenuitate, the poorly defined apertural area constituting a tenuitas. In some pollen, the aperture may be covered by a thickened lid or operculum, resulting in an operculate aperture.

*Aperture Position.*—Although some or all members of approximately 50 families of angiosperms have mature pollen grains shed as dyads, tetrads, polyads, or other large pollen-units (cf., below), most pollen as observed at maturity within the anther locules of the stamen consists of solitary grains or monads. However, since pollen always results from meiosis of pollen mother cells (PMC's), all pollen grains are at one time or another united together as members of a meiotic pollen tetrad. This fact allows certain dimensions of even a solitary pollen grain or monad to be defined in terms of the spatial relationships of the four grains of the pollen tetrad of which it was previously a member. Individual pollen grains may thus be likened to a globe with poles and an equator (Fig. 1a). The following definitions are derived from such an analogy. The polar axis of a pollen grain is defined as the line passing through the center of the grain from the outside to the center of the pollen tetrad (or to the center of the meiotic tetrad at the time of its formation in the case of solitary grains). The equatorial plane of a pollen grain, which contains two or more equatorial axes, perpendicularly bisects the polar axis and forms the boundary (equator) between the outer distal and inner proximal faces of the grain. The distal pole of a pollen grain faces away from the meiotic



tetrad, while the proximal pole is directed inward, facing the center of the tetrad. The single most important taxonomic-phylogenetic feature of pollen apertures is that they are not located randomly upon the surface of the pollen grain, but usually have very definite placement with reference to its poles and equator. Determination of absolute pollen grain polarity (cf. below) and with it absolute aperture position (i.e., knowledge of aperture position with reference to distal versus proximal pole or with reference to elongate equatorial apertures being either perpendicular or parallel to the equator) is of special importance in determining certain aperture types (e.g., anasulcate versus catasulcate or dicolpate versus disulculate, cf. below) and hence possibly aperture homologies. The determination of absolute aperture position in species with tetrads at maturity is quite straightforward. In taxa with solitary grains, however, the correct determination of absolute aperture position may be somewhat more difficult—one must either rely on comparative studies of related taxa with permanent tetrads or study cytologically the development of immature pollen tetrads before the grains separate. In practice, moreover, one frequently relies on apparent pollen grain polarity and symmetry axes (cf. below) to infer the position of apertures.

With respect to their position, three basic types of apertures may be recognized: (1) polar apertures located at or toward the poles, (2) equatorial apertures located on or at the equator, and (3) global apertures more or less uniformly scattered over the surface of the pollen grain. Polar apertures in turn may be classified with regard to the pole upon which the aperture is located, i.e., distal-polar or ana-aperturate if the aperture is located at or toward the distal pole and proximal-polar or cata-aperturate if the aperture is at or toward the proximal pole. With regard to position, elongate or ring-like apertures may be characterized further as meridional or latitudinal. Meridional (or longitudinal) apertures have their long axis perpendicular to the equator of the pollen grain and go through both poles (or would if extended), while latitudinal (or transverse) apertures have their long axis on or parallel to the equator (i.e., perpendicular to the polar axis) and would not go through the poles even if extended. The prefixes axi-, zoni-, and pan- are used, respectively, to refer to apertures located at or toward the poles, on or at the equator, and over the entire pollen surface, while the prefixes ana- and cata- refer to polar apertures which are distal-polar or proximal-polar. The prefix zona- is used to refer to a ring- or band-like aperture.

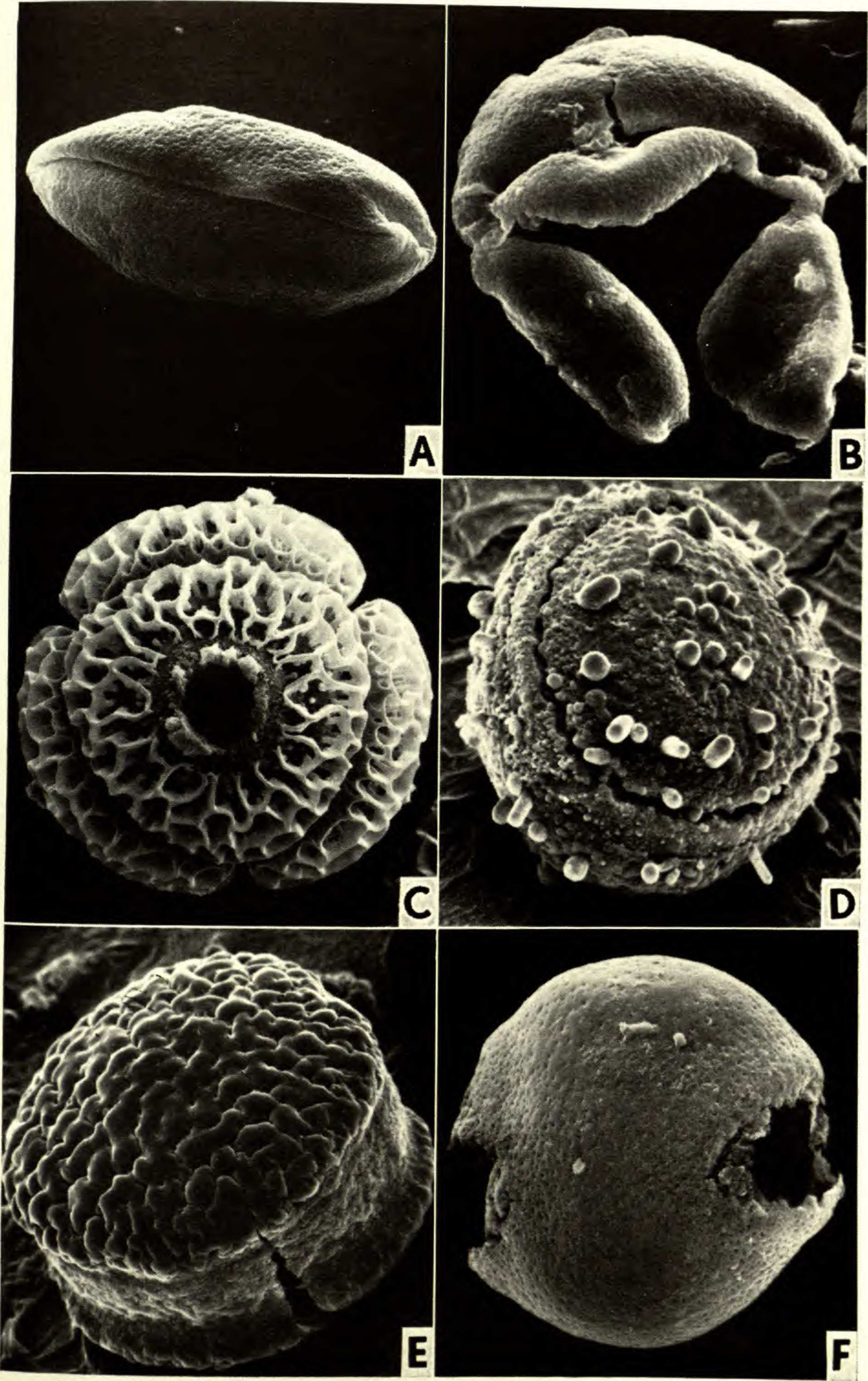
Apertures also possess a relative tetrad position, i.e., the position of each aperture of a given pollen grain relative to the position of the apertures of the other pollen grains of the pollen tetrad of which the particular pollen grain is a

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FIGURE 2. Polar and equatorial pollen apertures.—A. Anasulcate pollen;  $\times$  ca. 820 (*Magnolia fraseri* Walt.; Magnoliaceae). Presumed distal-polar view.—B. Anatrivotomosulcate pollen;  $\times$  ca. 820 (*Pseudoxandra coriacea* R. E. Fries; Annonaceae). Two grains of a permanent tetrahedral tetrad.—C. Anaulcerate pollen;  $\times$  ca. 1340 (*Drimys confertifolia* Phil.; Winteraceae). Grains in a permanent tetrahedral tetrad.—D. Anazonasulcate pollen;  $\times$  ca. 1660 (*Nymphaea amazonum* Mart. & Zucc.; Nymphaeaceae). Presumed distal-polar view.—E. Zonizonasulcate pollen;  $\times$  ca. 1240 (*Nymphaea violacea* Lehm.; Nymphaeaceae).—F. Disulculate pollen;  $\times$  ca. 1160 (*Calycanthus floridus* L.; Calycanthaceae). Presumed equatorial view with polar axis vertical and equatorial plane horizontal.







member. Single, polar, elongate, furrow-like apertures, which most commonly occur on pollen grains in tetragonal tetrads (cf. below), are generally found in an interplanar tetrad position, i.e., with the long axis of each furrow-like aperture more or less perpendicular to the plane of the tetrad (Fig. 1c), less frequently in a planar position, i.e., with the long axis of each furrow-like aperture in the same plane as the pollen grains of the tetrad itself (Fig. 1b; Walker, 1974c). Pollen grains with three equidistant equatorial apertures, which are the most common type of angiosperm pollen grains and which generally occur in tetrahedral tetrads (cf. below), almost always have their apertures in an interradian position, i.e., the apertures meet at points where only two grains of the tetrad are in contact, in six groups of two apertures each (Fig. 1e), while such apertures very rarely occur in a radial position, i.e., the apertures meet at the points where three grains of the tetrad are in contact, in four groups of three apertures each (Fig. 1d). Arrangement of apertures in the former tetrad position has been referred to as "Fischer's rule," while arrangement in the latter position has been called "Garside's rule" (cf. Erdtman, 1969).

*Polar Apertures (Axi-aperturate Pollen).*—Polar aperture types include sulcate pollen with a single, polar, elongate, furrow-like aperture known as a sulcus (plural, sulci), ulcerate pollen with a single, polar, rounded, pore-like aperture known as an ulcus (plural, ulci), and axizonasulculate pollen with a single, latitudinal, ring- or band-like aperture encircling one of the poles known as an axizonasulculus (plural, axizonasulculi). If the above apertures are known to be located at or toward the distal pole (i.e., are ana-aperturate), the pollen may be described respectively as anasulcate (Fig. 2A), anaulcerate (Fig. 2C), and anazonasulculate (Fig. 2D). Pollen with corresponding proximal-polar (i.e., cata-aperturate) apertures would be catasulcate, cataulcerate, or catazonasulculate. Except for some catasulcate-cataulcerate pollen in the Annonaceae (Walker, 1971b, 1972b), all other sulcate or ulcerate angiosperm pollen appears to be distal-polar (e.g., Bailey & Swamy, 1949; Canright, 1953; Swamy, 1949; Wilson, 1964), and therefore sulcate or ulcerate apertures are probably best considered to be distally located (i.e., anasulcate or anaulcerate) unless proved otherwise. Sometimes anasulcate pollen may be three-armed or anatrachotomosulcate (Fig. 2B), or more rarely even 4-armed or tetrachotomosulcate. Sulci, trichotomosulci, and ulci all have their center located at one of the poles, while axizonasulculi run around one of the poles. All polar apertures are essentially meridional with the exception of axizonasulculate apertures which are latitudinal. Axi-aperturate pollen is almost always mono-aperturate.

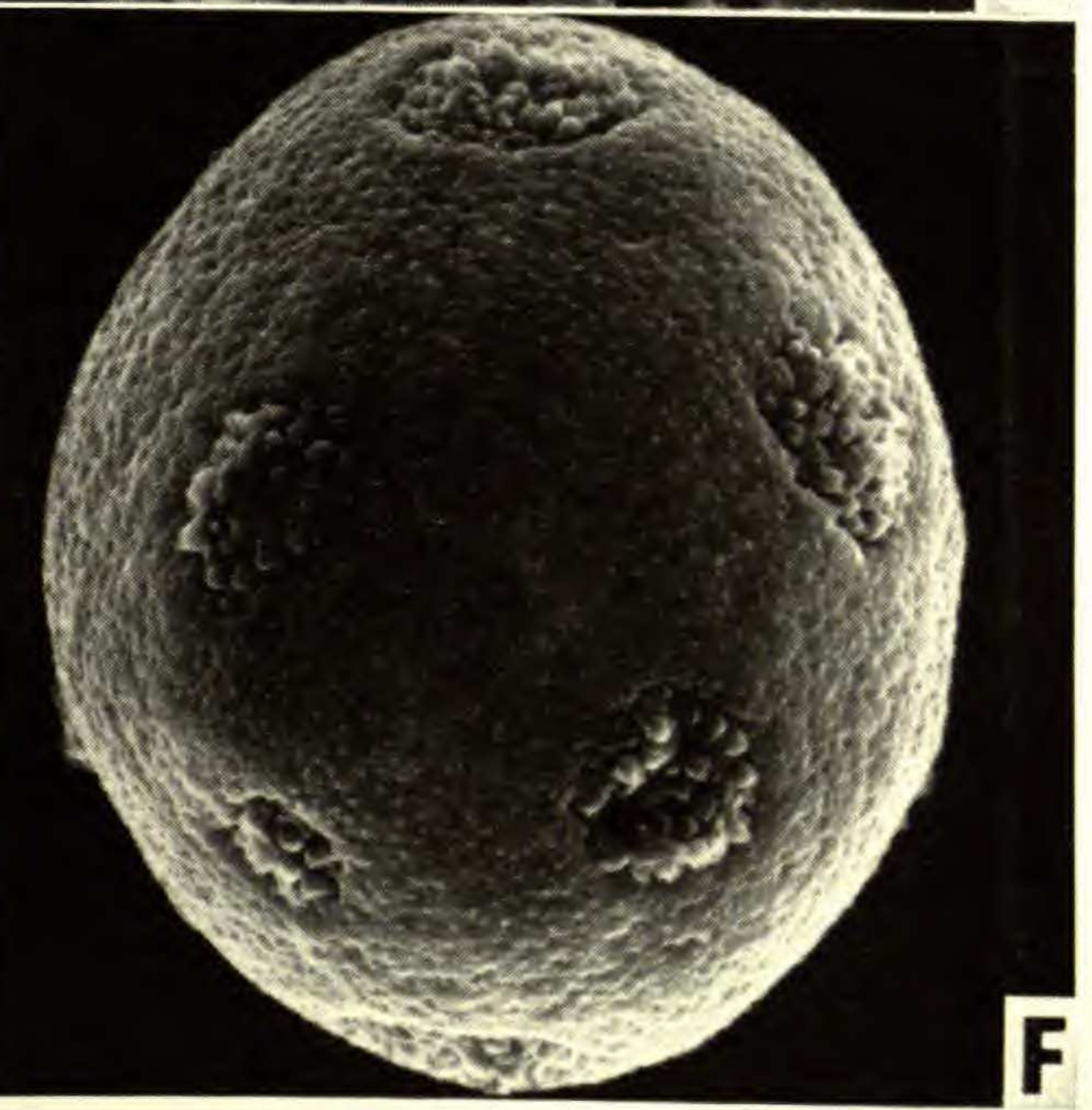
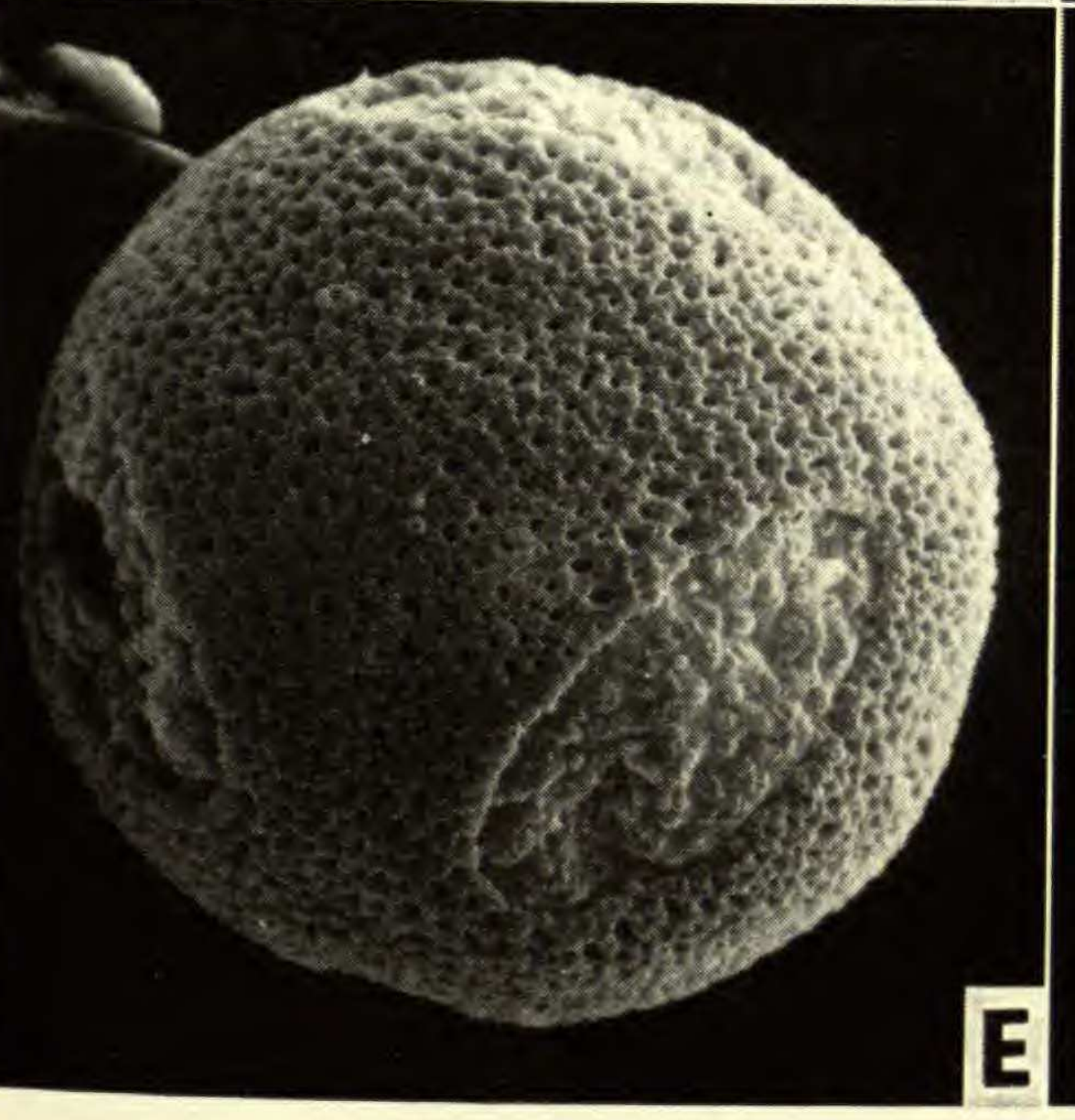
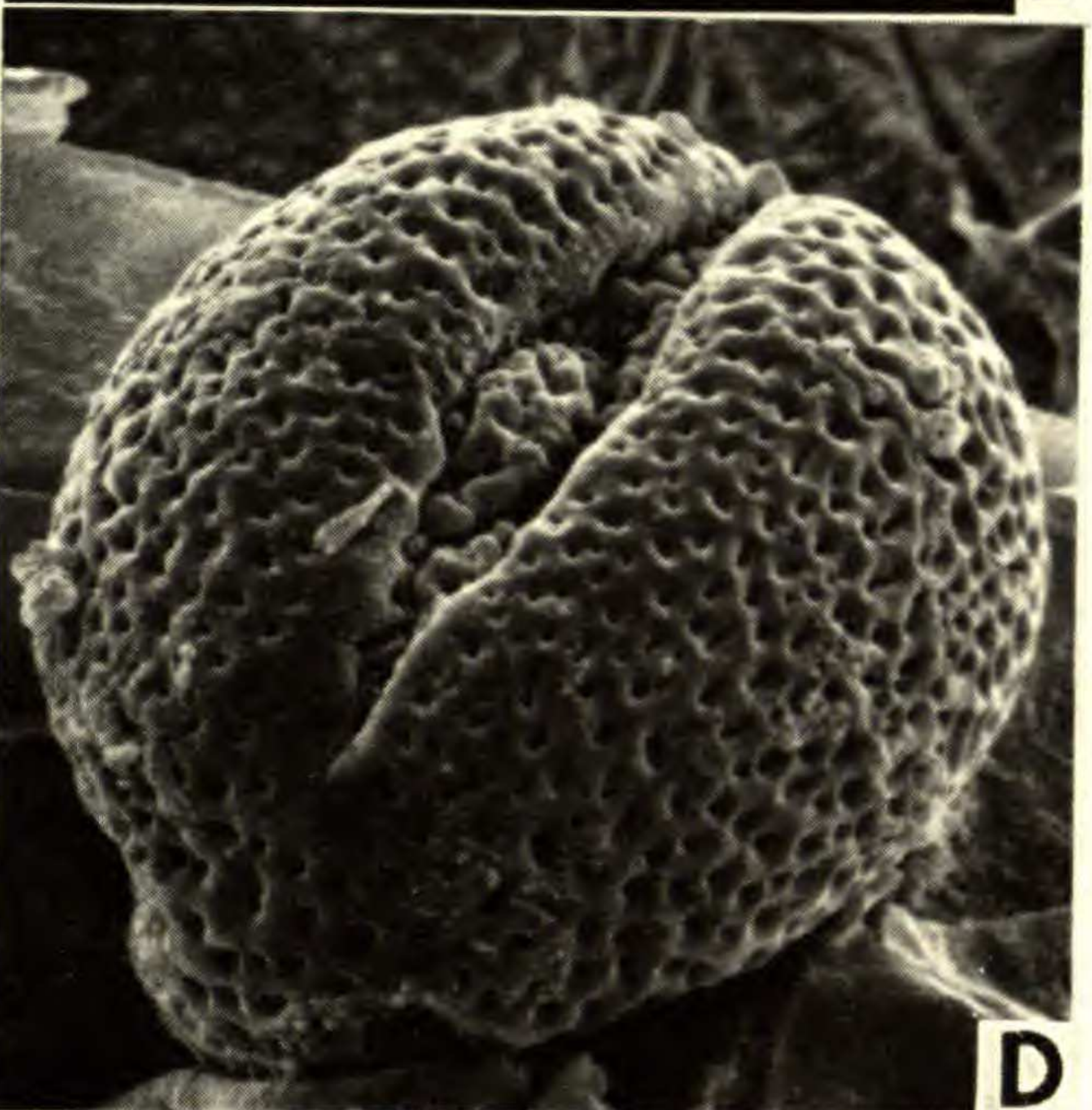
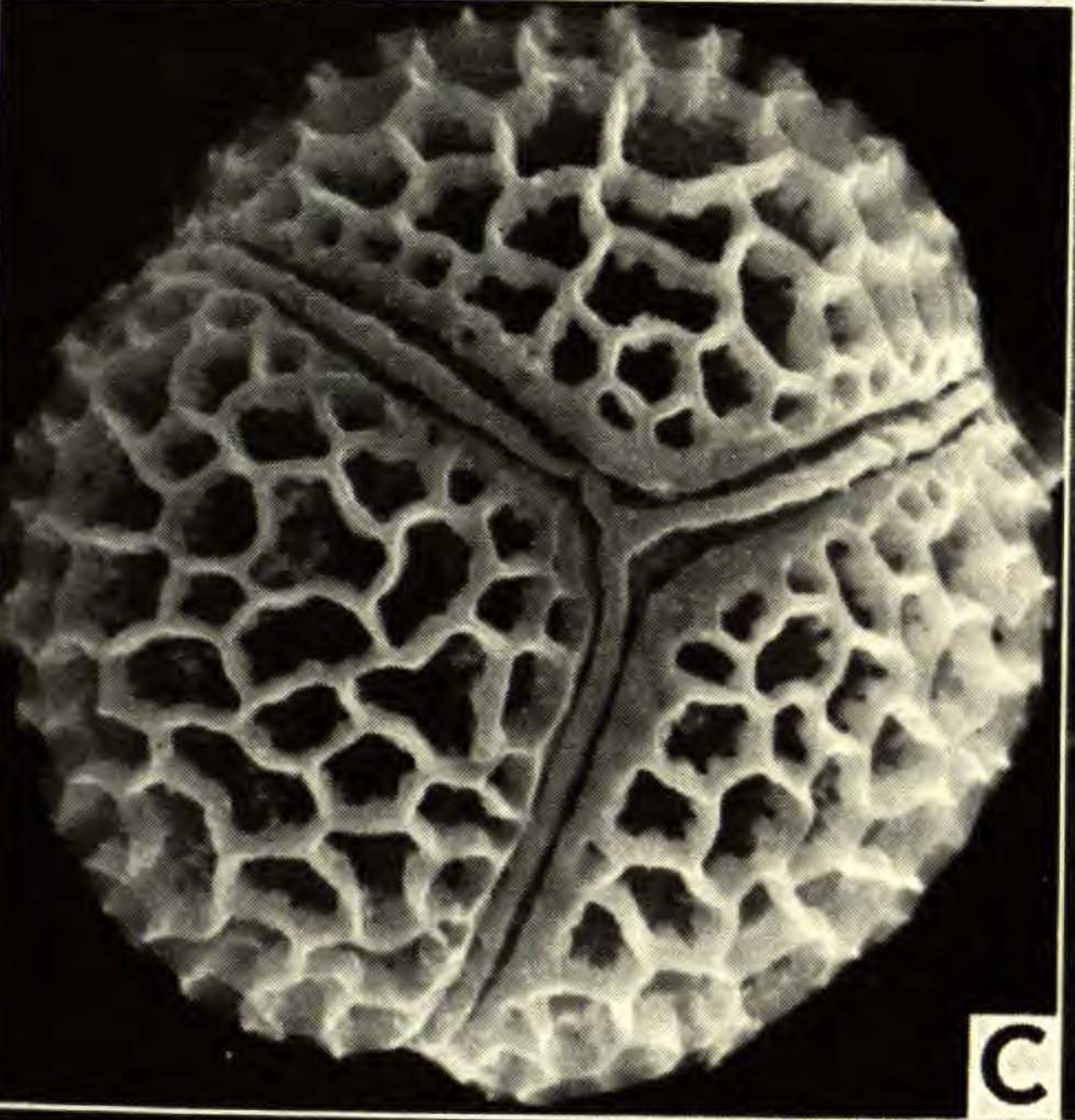
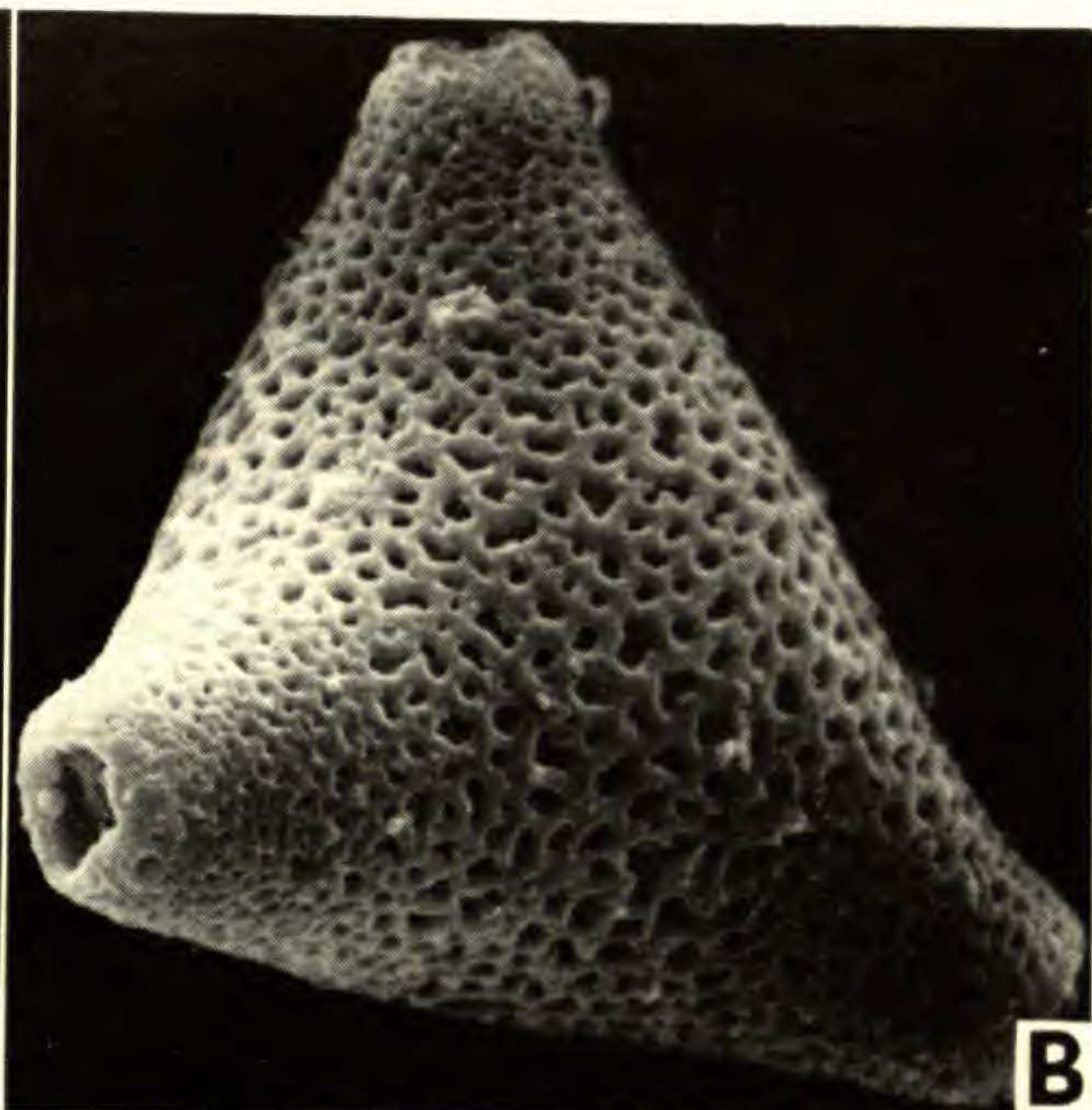
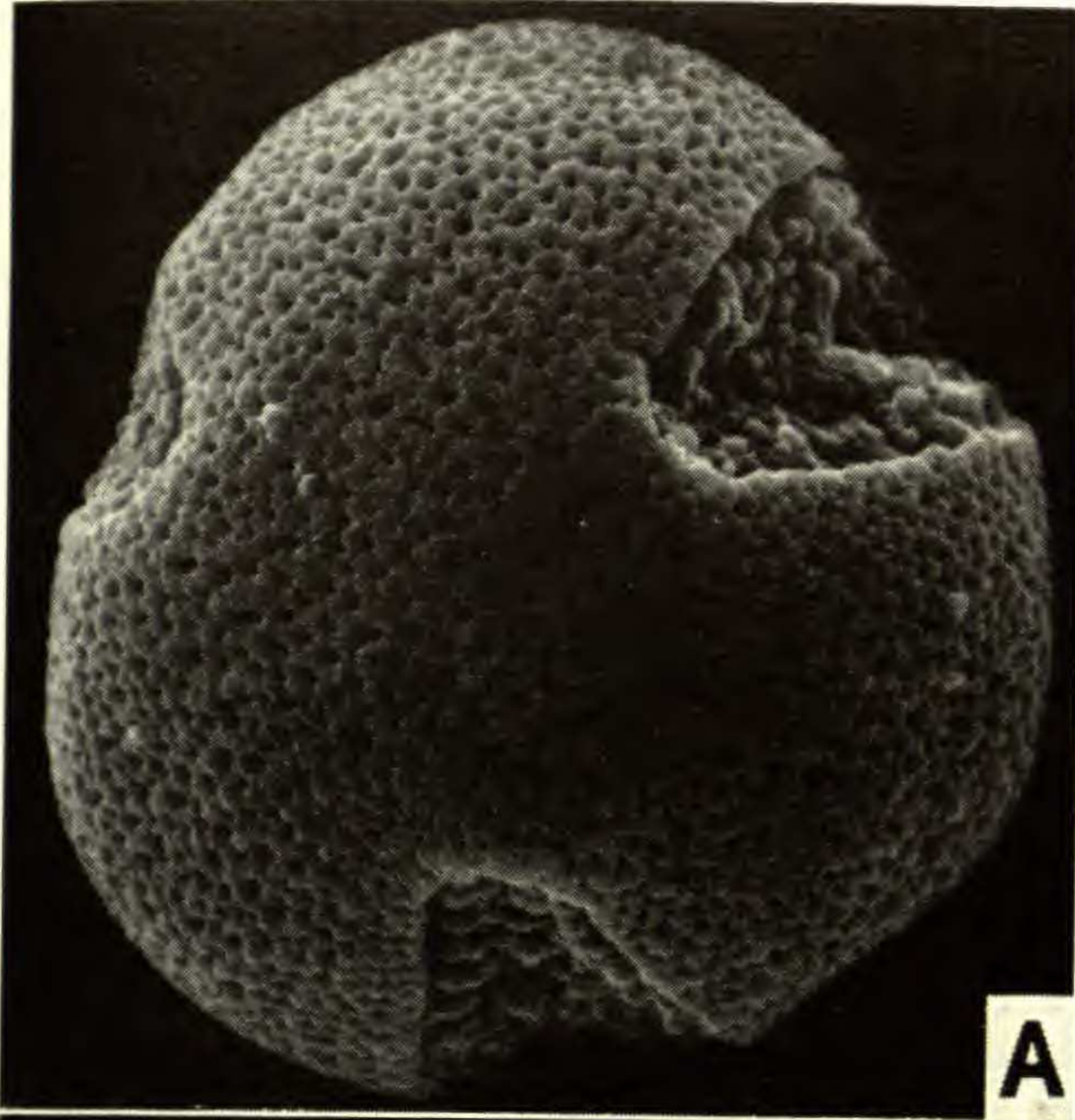
*Equatorial Apertures (Zoni-aperturate Pollen).*—Equatorial aperture types

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FIGURE 3. Equatorial and global pollen apertures.—A. Tricolpate pollen;  $\times$  ca. 1890 (*Euptelea pleiosperma* Hook.f. & Thomas; Eupteleaceae). Polar view.—B. Triporate pollen;  $\times$  ca. 900 (*Euplassa inaequalis* (Pohl) Engl.; Proteaceae). Polar view.—C. Syntri-colpate pollen;  $\times$  ca. 2240 (*Schisandra grandiflora* (Wall.) Hook.f. & Th.; Schisandraceae). Presumed distal-polar view.—D. Tricolporate pollen;  $\times$  ca. 3350 (*Limacia sagittata* Oliv.; Menispermaceae). Equatorial view.—E. Rugate pollen;  $\times$  ca. 2530 (*Euptelea polyandra* Sieb. & Zucc.; Eupteleaceae).—F. Forate pollen;  $\times$  ca. 2800 (*Trimenia papuana* Ridl.; Trimeniaceae).







include colpate pollen, sensu stricto,<sup>5</sup> (Fig. 3A) with meridional, elongate, furrow-like apertures located equidistantly at the equator and normally bisected by the equatorial plane known as colpi (singular, colpus), porate pollen, sensu stricto,<sup>5</sup> (Fig. 3B) with round, pore-like apertures located equidistantly on the equator known as pores (singular, pore), sulculate pollen (Fig. 2F) with latitudinal, elongate, furrow-like apertures located equidistantly on the equator known as sulci (singular, sulcus), and zonizonasulculate pollen (Fig. 2E) with a latitudinal, ring- or band-like, encircling aperture running around the equator known as a zonizonasulculus (plural, zonizonasulculi). Pollen with equatorial, rounded apertures derived from sulci (i.e., the pore-like apertures are latitudinal-derived) may be described as ulculate, with the pore-like apertures being ulculi (singular, ulculus). The pores in porate pollen, on the other hand, are not derived through shortening of previously existing sulci, but are basically meridionally derived via shortening of colpi instead of sulci. If a pollen grain should have an encircling, ring-like aperture that is latitudinal and clearly not meridional, but no more is known about its exact position (i.e., whether it is axizonasulculate, anazonasulculate, catazonasulculate, or zonizonasulculate), it should be described simply as zonosulculate. A pollen grain with a single, encircling, ring- or band-like aperture which is meridional rather than latitudinal may be described as zonosulcate, with the aperture being a zonosulcus (plural, zonosulci). Zoni-aperturate pollen, unlike axi-aperturate pollen, usually has more than one aperture (except for zonizonasulculate and zonosulcate pollen which is mono-aperturate). Sulculate-ulculate pollen appears to be almost always di-aperturate (i.e., disulculate, diulculate), while colpate and porate pollen is usually tri-aperturate (i.e., tricolpate, triporate), less frequently di-aperturate (e.g., dicolpate, diporate). Although much less frequent than tricolpate, colpate pollen may also be 4-colpate, 5-colpate, or 6-colpate, more rarely 7–12-colpate or greater than 12-colpate. In some colpate pollen, all or some of the colpi may be fused at one or both poles resulting in different types of syncolpate pollen grains (Fig. 3C).

*Global Apertures (Pan-aperturate Pollen).*—Global apertures may be elongate and furrow-like (rugae; singular, ruga) resulting in rugate pollen (Fig. 3E), or round and pore-like (foramina; singular, foramen) resulting in forate pollen grains (Fig. 3F). Although rugate pollen may have six or less apertures, forate pollen usually has more than six apertures and frequently more than 12 apertures.

*Miscellaneous Aperture Types.*—There are a number of miscellaneous aperture types which are frequently difficult to categorize, e.g., pollen of the rosaceous genera *Griehum* and *Neurada* (cf. Erdtman, 1966) which appears to possess 3-armed apertures at both poles (which may have originated from bipolarly fused tricolpate pollen that subsequently lost connecting parts of the colpi in the region of the equator). Pollen of *Commelinantia* (Commelinaceae) exemplifies another distinctive aperture type (cf. Rowley & Dahl, 1962). Another rare

<sup>5</sup> The terms colpate and porate have been used by a number of authors in a broad sense to refer to any apertures irrespective of position which are respectively elongate and furrow-like or round and pore-like. Here and elsewhere in this paper, unless otherwise noted, these terms are used in the more restricted sense to refer solely to meridionally elongate or meridionally derived rounded apertures which are equatorially located.



aperture type occurs in the "3-ulcerate" pollen of some monocotyledons (e.g., palms) which have three, equidistant, pore-like apertures situated around one pole that may have been derived from a trichotomosulcus. A more frequently met miscellaneous aperture type is represented by spiraperturate pollen grains which have a number of elongated, furrow-like apertures that are spirally arranged. Also, apertures infrequently may be borne on more or less rounded, protruding, dome-like areas, thus producing aspidote pollen. If a chamber is formed in such pollen grains between an outer and inner aperture opening, it is known as an atrium (plural, atria). Pollen grains with locally thickened areas of the exine which extend in sweeping curves from aperture to aperture (arci; singular, arcus) may be described as arcuate.

*Aperture Structure.*—Pollen apertures may be simple or compound. Simple apertures have more or less uniform aperture membranes, while compound or orate apertures (Fig. 3D) possess specially delimited areas of the aperture membrane known as ora (singular, os). Most compound apertures are mono-orate with one os per aperture; however, diorate pollen with two ora per aperture does occur, although rather infrequently. Ora are usually, although not always, more or less rounded. Extended or elongate ora may be either transversely (latitudinally) elongated and lalongate or longitudinally (meridionally) elongated and lolongate. The following aperture types are exclusively simple: sulcate, trichotomosulcate, zonasulcate, ulcerate, sulculate, ulculate, and zonasulculate. Rugate and forate pollen may have either simple or compound apertures. Colpate and porate pollen grains may have simple or compound apertures, with compound apertures being the more frequent. Compound apertures are designated by introducing the syllable -or- into the terms describing the corresponding simple apertures. Thus, colpate, porate, rugate, and forate pollen with compound apertures would be called colporate, pororate, rugorate, and fororate. Of these, the most common type of compound-aperturate pollen is represented by colporate pollen grains, which have pore-like structures in the center of the colpi. Colporoidate pollen would have well developed colpi with weakly developed ora (oroids), while colpoidorate pollen would have weakly developed colpi (colpoids) with well developed ora. Similarly, pororoidate pollen would have well developed pores with the ora weakly developed, while poroidorate pollen has weakly developed pores (poroids) with well developed ora. The main characteristics of the basic types of apertures found in angiosperm pollen are summarized in Table 1.

*Evolution of Pollen Aperture Types.*—The evolution of apertures in pollen grains was one of the major advances of seed plants, and aperture type (along with the pollen wall) constitutes one of the most important phylogenetic pollen characters. The spores of pteridophytes, in the strict sense, do not possess apertures; however, their spores do have analogous, weakened areas on the proximal pole called tetrad scars by which they often open. These scars may be either trilete (triradiate or Y-shaped) or monolete (straight). It was in gymnospermous plants that the first true apertures evolved. Certain fossil gymnosperm pollen grains (e.g., the pollen grains of some pteridosperms) still retain a trilete tetrad scar on the proximal face which is homologous to the tetrad scar of



TABLE 1. Main characteristics of basic angiosperm pollen aperture types.

| Aperture Shape | Aperture Position                | Number of Apertures | Aperture Type <sup>a</sup>   |
|----------------|----------------------------------|---------------------|------------------------------|
| Furrow-like    | Unknown                          | 1–many              | Colpate, sensu lato          |
|                | Polar (axi-aperturate)           | 1                   | (Mono)Sulcate                |
|                | Distal-polar (ana-aperturate)    | 1                   | Anasulcate <sup>b</sup>      |
|                | Proximal-polar (cata-aperturate) | 1                   | Catasulcate                  |
|                | Equatorial (zoni-aperturate)     |                     |                              |
|                | Meridional (longitudinal)        | 2–many              | Colpate, sensu stricto       |
|                | Latitudinal                      | 2                   | (Di)Sulculate                |
|                | Global (pan-aperturate)          | 4–many              | Rugate                       |
| Pore-like      | Unknown                          | 1–many              | Porate, sensu lato           |
|                | Polar (axi-aperturate)           | 1                   | (Mono)Ulcerate               |
|                | Distal-polar (ana-aperturate)    | 1                   | Anaulcerate                  |
|                | Proximal-polar (cata-aperturate) | 1                   | Cataulcerate                 |
|                | Equatorial (zoni-aperturate)     |                     |                              |
|                | Meridional-derived               | 2–many              | Porate, sensu stricto        |
|                | Latitudinal-derived              | 2                   | (Di)Ulcuate                  |
|                | Global (pan-aperturate)          | 4–many              | Forate                       |
| Ring-like      | Unknown                          | 1                   | Zonate                       |
|                | Polar (axi-aperturate)           | 1                   | Axizonasulculate             |
|                | Distal-polar (ana-aperturate)    | 1                   | Anazonasulculate             |
|                | Proximal-polar (cata-aperturate) | 1                   | Catazonasulculate            |
|                | Equatorial (zoni-aperturate)     |                     |                              |
|                | Meridional                       | 1                   | Zonasulcate                  |
|                | Latitudinal                      | 1                   | Zonizonasulcate <sup>c</sup> |

<sup>a</sup> Sulcate, trichotomosulcate, ulcerate, sulculate, ulculate, zonasulculate, and zonasulcate apertures are always simple. Colpate, porate, rugate, and forate apertures may be simple or compound.  
<sup>b</sup> Anasulcate pollen grains may occasionally be 3-armed or anatrachotomosulcate, more rarely 4-armed or tetrachotomosulcate.  
<sup>c</sup> A ring-like aperture that is clearly latitudinal and not meridional (but unspecified as to being around one of the poles or the equator) may be described simply as zonasulcate.

pteridophyte spores (Wodehouse, 1935; Chaloner, 1970). The first true apertures, however, evolved at the distal pole (facing outward in the meiotic tetrad) and were furrow-like (sulcate). With reference to angiosperm pollen, two basic aperture types are generally recognized (Fischer, 1890; Wodehouse, 1935; Kuprianova, 1967, 1969): *monosulcate* (*monocolpate*, sensu lato, of some authors)—with a single, furrow-like aperture located at one of the poles (usually the distal), and *tricolpate*—with three, equidistant, furrow-like apertures that are perpendicular to the equator (i.e., meridional). However, since it is clear that in at least two different families of the Magnoliidae (Chloranthaceae, Aristolochiaceae), monosulcate pollen evolved into polycolpate (or polyporate) pollen, i.e., pollen with more than three colpi or pores, via an inaperturate intermediary form without going through a tricolpate stage (cf. Walker, 1974c), a more general distinction in terms of *evolutionary grade* would be between sulcate and simply colpate pollen. Colpate pollen is essentially restricted to dicotyledonous angiosperms,



while sulcate pollen is found in gymnosperms, the monocots, and some ranalean dicots.

Angiosperm pollen is thus divided into two fundamentally different types—that which is *monosulcate* or *monosulcate-derived* versus pollen which is *tricolpate* or *tricolpate-derived*, depending on whether their ancestral forms are believed to have been monosulcate or tricolpate. Although in a sense all angiosperm pollen other than monosulcate pollen itself is “monosulcate-derived,” tricolpate and tricolpate-derived pollen is recognized as distinct from other “monosulcate-derived pollen” because tricolpate pollen (and its derivative forms) is the main type of pollen found in most dicotyledons, is essentially restricted to dicotyledonous angiosperms, and has served as the basis for a radiation of “tricolpate-derived” aperture types. Monosulcate-derived pollen also differs from tricolpate-derived pollen, other than in aperture number and position (monosulcate-derived pollen usually, but certainly not always, having one polar aperture, while tricolpate-derived pollen usually has three equatorial apertures), in that it always has simple apertures, while most tricolpate-derived pollen has compound apertures. Monosulcate-derived apertures include polar aperture types such as found in trichotomosulcate, ulcerate, and axizonasulculate pollen, as well as some equatorial aperture types such as found in sulculate, ulculate, zonizonasulculate, and zonosulcate pollen. Tricolpate-derived apertures (e.g., tricolporate, triporate, etc.), on the other hand, are almost always equatorial. Global apertures may be either monosulcate- or tricolpate-derived (e.g., forate pollen grains in the monocotyledonous family Alismataceae and the non-magnoliid dicot family Malvaceae), although rugate pollen appears to be restricted to the non-magnoliid dicots, i.e., is tricolpate-derived. Inaperturate pollen likewise may be either monosulcate- or tricolpate-derived. The polycolpate/polyporate pollen found in the Chloranthaceae and Aristolochiaceae must be considered unique in being clearly monosulcate-derived; all other colpate pollen in dicotyledonous angiosperms appears to be tricolpate or tricolpate-derived. By contrast, monosulcate or monosulcate-derived pollen is unknown among non-magnoliid dicotyledons, being restricted, as previously indicated, to some ranalean dicots, the monocotyledons, and gymnosperms.

A single, furrow-like aperture located at the distal pole of the pollen grain (an anasulcus) is undoubtedly the primitive (ancestral) aperture type in the angiosperms (Walker, 1974c). This is borne out by several lines of evidence. First, anasulcate pollen is found in, and is widespread among, extant and fossil gymnosperms. Secondly, within the angiosperms themselves, anasulcate pollen is restricted to the otherwise most primitive subclass of dicotyledons, the Magnoliidae, and to the monocots, the bulk of dicotyledonous angiosperms having tricolpate or tricolpate-derived aperture types. Also, anasulcate pollen occurs in what are believed to be the more primitive members *within* the subclass Magnoliidae. Finally, monosulcate pollen has been shown to precede other angiospermous aperture types in the fossil record (Doyle, 1969; Muller, 1970).

Within primitive ranalean dicots (subclass Magnoliidae), anasulcate pollen has given rise more or less directly to the following aperture types (Fig. 4; Walker, 1974c): anatrachotomosulcate, zonosulculate, anaulcerate, catasulcate-



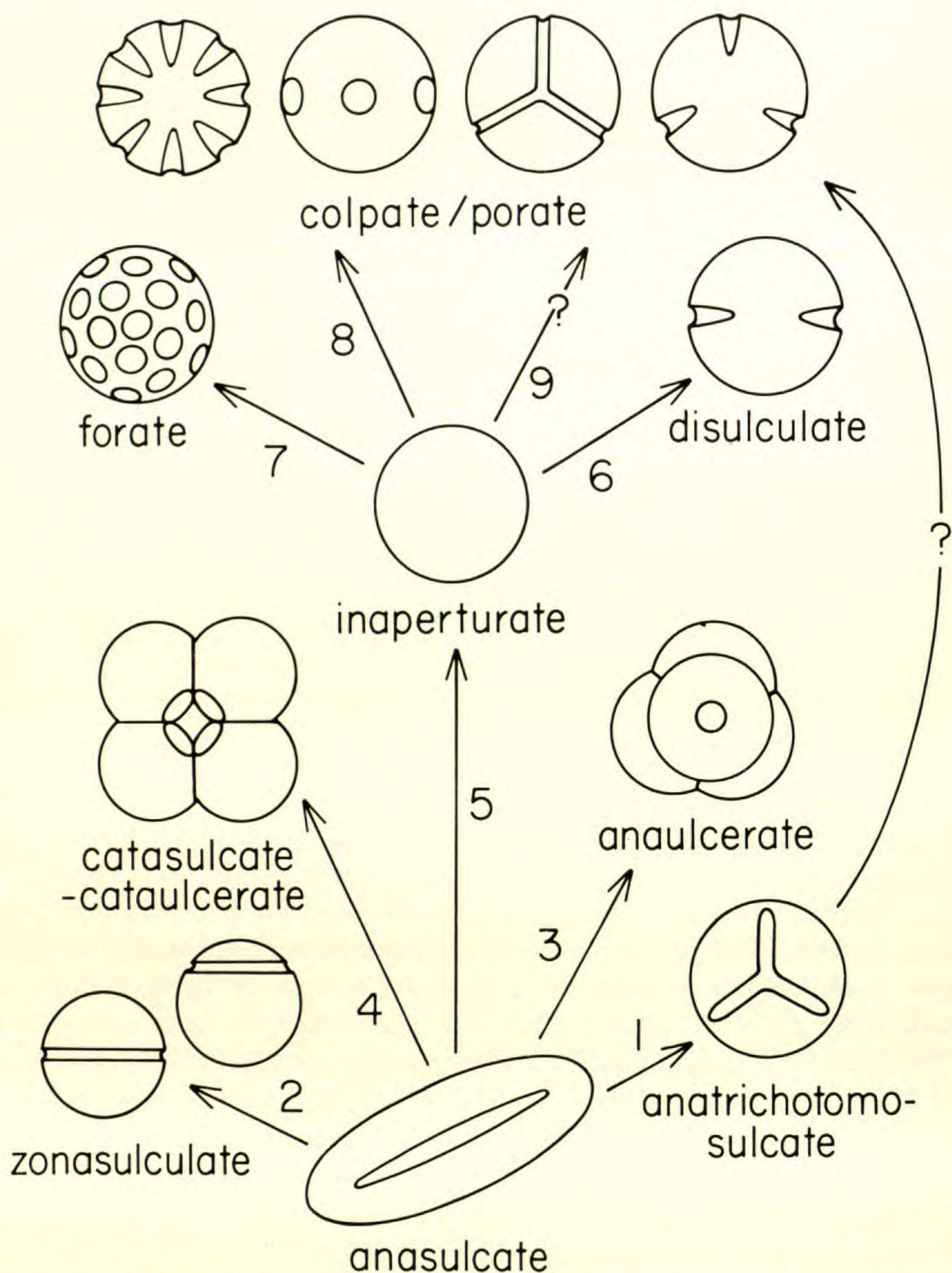


FIGURE 4. Major evolutionary trends in pollen apertures of magnoliid dicots. Anasulcate, anatrictotomosulcate, anaulcerate, polycolpate, syntricolpate, and tricolpate pollen shown in polar view; zonasulcate, catasulcate-cataulcerate, disulcate, and triporate pollen shown in equatorial view. See text for discussion.

cataulcerate, and inaperturate (and thence to disulcate and forate pollen). Evidence from extant primitive angiosperms suggests that inaperturate, not trictotomosulcate pollen (cf. Straka, 1963; Wilson, 1964), was the ancestral pollen type which gave rise to the uniquely angiospermous (dicotyledonous) colpate pollen aperture. From the basic tricolpate form of this colpate pollen the diversity of non-magnoliid aperture types such as 5-colpate, 6-colpate, porate, colpate, pororate, rugate, forate, etc. appear to have evolved.



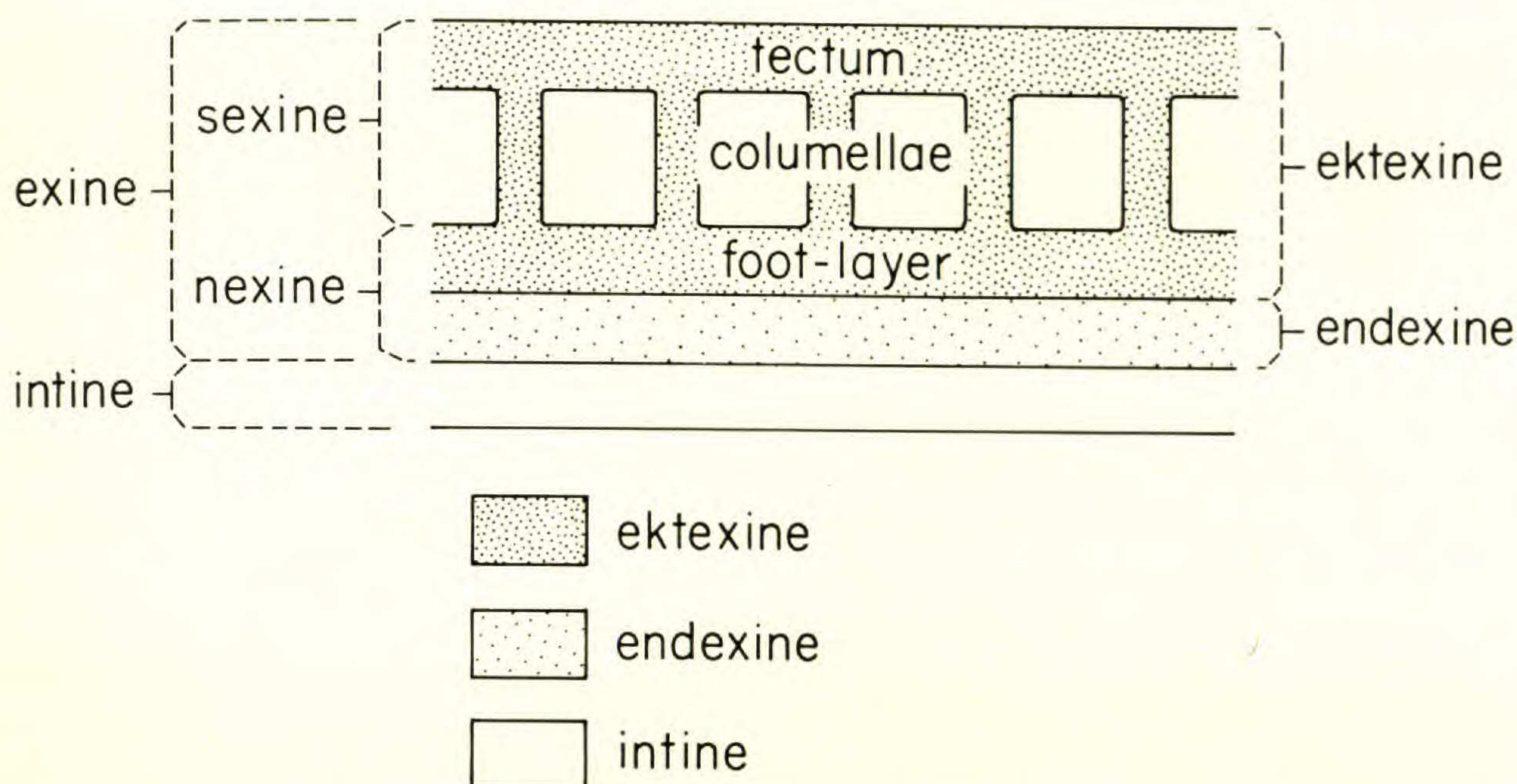


FIGURE 5. Pollen wall stratification as observed in a typical angiosperm pollen grain. This particular diagram represents a cross-section in a nonapertural area of a tectate-imperforate, non-acetolyzed pollen grain that has endexine and a foot-layer.

#### POLLEN WALL ARCHITECTURE

The nature of the pollen wall itself provides a multitude of phylogenetically important characters. However, probably no other palynological character has been responsible for so much terminological confusion as pollen wall morphology (cf. Wittmann & Walker, 1965; Van Campo et al., 1967; Manten, 1970; Walker, 1974b). Pollen wall architecture is here proposed to encompass all aspects of pollen wall morphology, i.e., internal structural components as well as external surface elements, and is specifically created as a broad term to include pollen wall stratification as well as exine structure and sculpturing.

*Pollen Wall Stratification.*—Pollen wall stratification refers to the various layers (strata) present in the pollen wall, as observed morphologically, chemically, and/or developmentally. The pollen wall of most angiosperm pollen grains (Fig. 5) consists of two fundamentally different layers: an inner, more or less cellulosic layer (the intine) which is usually destroyed upon acetolysis (cf. Faegri & Iversen, 1964); and an outer, acetolysis-resistant layer (the exine), which is composed of oxidative polymers of carotenoids and/or carotenoid esters known as sporopollenin (Shaw, 1971). However, since most modern pollen is prepared for study by acetolysis and the intine is lacking in fossil pollen, study of the pollen wall usually consists of the study of the exine.

*Exine Stratification.*—The exine of acetolyzed angiosperm pollen grains as observed in the light microscope (Fig. 5) typically consists of two layers: an inner, basal layer or nexine ("nonsculptured exine"); and an outer layer or sexine ("sculptured exine"). In angiosperms, a "complete" sexine is two-layered and consists of internal, up-right, rod-like elements known as columellae (bacula) covered by a roof-like layer or tectum. In fact, the presence of a middle layer of distinct, well-defined columellae (i.e., pollen tectate), rather than an irregular spongy layer (i.e., pollen alveolate), appears to be one of the main features in



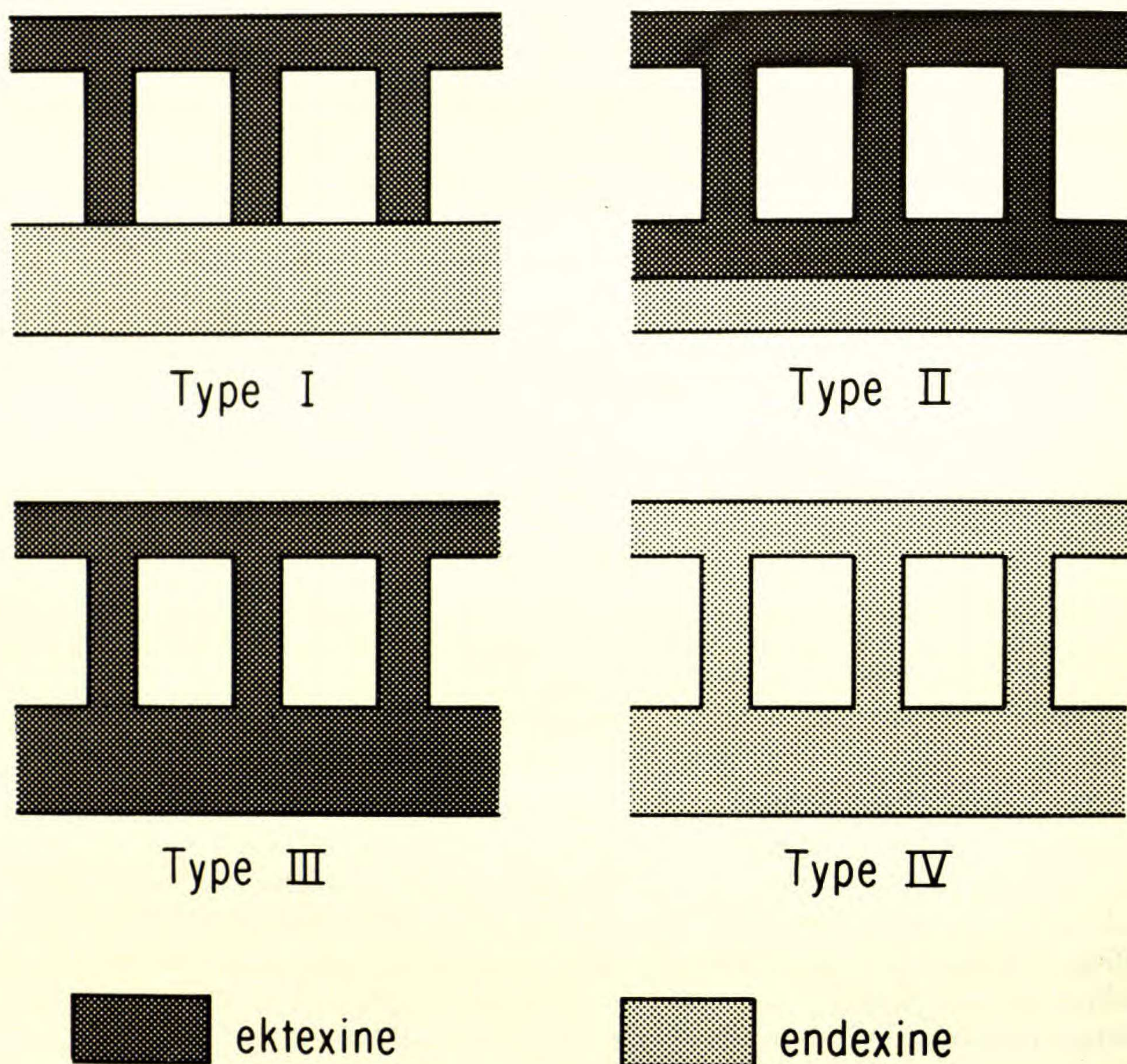


FIGURE 6. Exine stratification types. Diagrams represent cross-sections in nonapertural areas of tectate-imperforate, acetolyzed pollen grains. Type I exine is ektexinous-endexinous with no foot-layer. Type II exine is ektexinous-endexinous with a foot-layer. Type III exine is entirely ektexinous. Type IV exine is entirely endexinous.

which angiosperm exines differ in general from those of gymnosperms (Van Campo, 1971).

By proper staining and light microscopy (Faegri, 1956) or more readily with transmission electron microscopy (Larson et al., 1962; Larson, 1964), the exine in a number of angiosperms has been shown to be chemically differentiated into two distinct layers (which are also developmentally correlated), the outer such layer being called the ektexine and the inner the endexine (Fig. 5). Distribution of the chemically-developmentally defined ektexine-endexine with reference to the morphologically observed sexine-nexine permits envisionment of four basic exine stratification types (Fig. 6). In some pollen the ektexine may be equivalent to the sexine (with the endexine corresponding to the nexine), i.e., the nexine is entirely endexinous (exine stratification type I). However, in many taxa an outer layer of the nexine proves to be chemically (and developmentally) similar



to the sexine (columellae and tectum, if present) when examined with the transmission electron microscope or the light microscope if the proper staining has been used (e.g., Faegri, 1956; Leffingwell, Larson & Valencia, 1970). Such an outer zone of the nexine which is chemically like the sexine is called the foot-layer (pedium, sole, nexine-1) (Fig. 5), and in pollen grains of this kind the endexine corresponds only to an inner layer of the nexine (called nexine-2 by some authors), not the entire nexine, while the ectexine includes the sexine plus foot-layer, i.e., the nexine is composed of endexine and an outer ectexinous foot-layer (exine stratification type II). Occasionally the endexine itself may be further subdivided into two chemically different layers (Walker & Skvarla, unpublished). In other pollen the exine appears to be undifferentiated into chemically distinct layers; such chemically homogeneous exine may represent ectexine exclusively and grains of this type lack an endexine, i.e., the nexine is entirely ectexinous (exine stratification type III), or the exine may be essentially endexinous with little or no ectexine (exine stratification type IV). It should be stressed that normally the amount of ectexine to endexine differs in apertural versus nonapertural areas of the exine of a given pollen grain. In many species the aperture membrane appears to be made up solely of endexine or of endexine and greatly reduced ectexine, the latter being otherwise well-developed in the nonapertural areas of the exine. In some pollen by contrast, the endexine may be extremely thick beneath the apertural area of the exine, while much thinner or even lacking entirely under the rest of the exine. Although the exine as a whole is usually acetolysis-resistant, endexine appears to be less resistant to acetolysis than ectexine. This is probably the reason that the largely endexinous aperture membranes of pollen grains are frequently found broken in pollen that has been subjected to acetolysis (cf. Figs. 2B, 2C, 2F). In some morphologically inaperturate pollen grains (which commonly may not be acetolysis-resistant), the entire pollen surface may be largely endexinous and the whole pollen grain may actually correspond to the aperture membrane of a normal pollen grain (cf. Skvarla & Rowley, 1970). Finally, the intine itself frequently exhibits pronounced thickening below the aperture regions; such thickening of the intine is known as an oncus (plural, onci).

A fundamental concept relating to the pollen wall (in a stricter sense, the pollen exine) is the difference between internal structure and external sculpturing. In the "complete" sexine described above (cf. Fig. 5), the internal, rod-like columellae constitute *structure*, while any external elements located upon the tectum, such as spines, granules, etc., constitute *sculpturing*. Thus, a basic distinction is made in such pollen between internal *infratectal*<sup>6</sup> structural components and external *supratectal* sculpturing elements. As previously pointed out (Walker, 1971d), the most important palynological difference between the light and the scanning electron microscope is that the former instrument shows both structure and sculpturing in such "complete" or tectate pollen grains due to the penetration of light-waves (photons) and the ability of the light microscope to produce optical sections, while the scanning electron microscope with its less penetrating electrons shows only sculpturing.

<sup>6</sup> Infratectal structural components are located below the tectum (between it and the nexine); entities within the tectum itself would be described as intratectal.



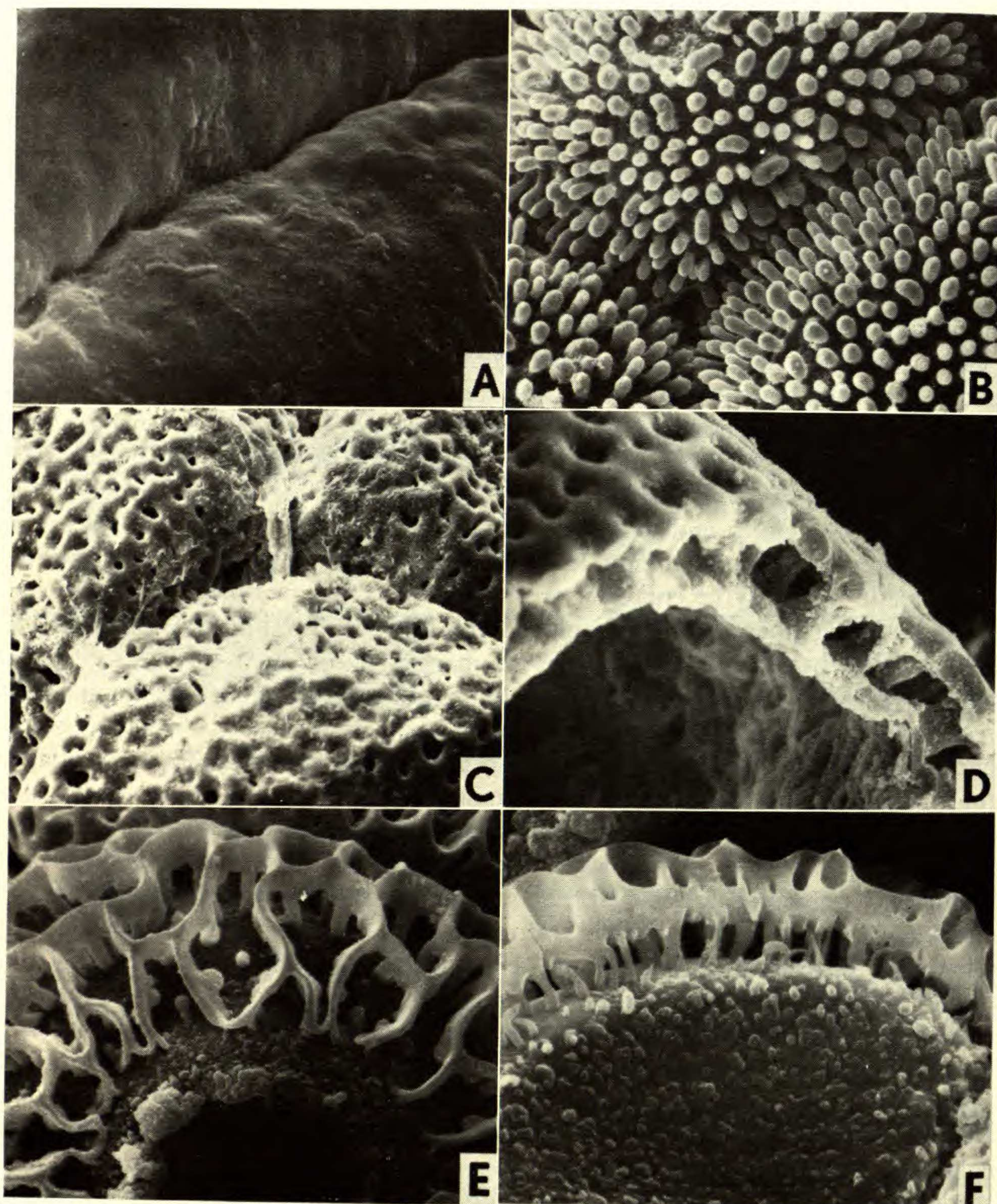


FIGURE 7. Basic angiosperm exine structure types.—A. Tectate-imperforate pollen (*Dialyanthera acuminata* Standl.; Myristicaceae). Surface view;  $\times$  ca. 3450.—B. Intectate pollen (*Trigynaea caudata* (R. E. Fries) R. E. Fries; Annonaceae). Partial surface view of a polyad;  $\times$  ca. 1360.—C–D. Tectate-perforate pollen (*Asimina pygmaea* (Bartr.) Dunal; Annonaceae).—C. Partial surface view of a tetrad;  $\times$  ca. 1500.—D. More or less cross-sectional view;  $\times$  ca. 3250.—E–F. Semitectate pollen (*Drimys confertifolia* Phil.; Winteraceae).—E. Partial surface view of two pollen grains of a permanent tetrad; hole at bottom is part of ulcerate aperture;  $\times$  ca. 3500.—F. More or less cross-sectional view;  $\times$  ca. 3400.



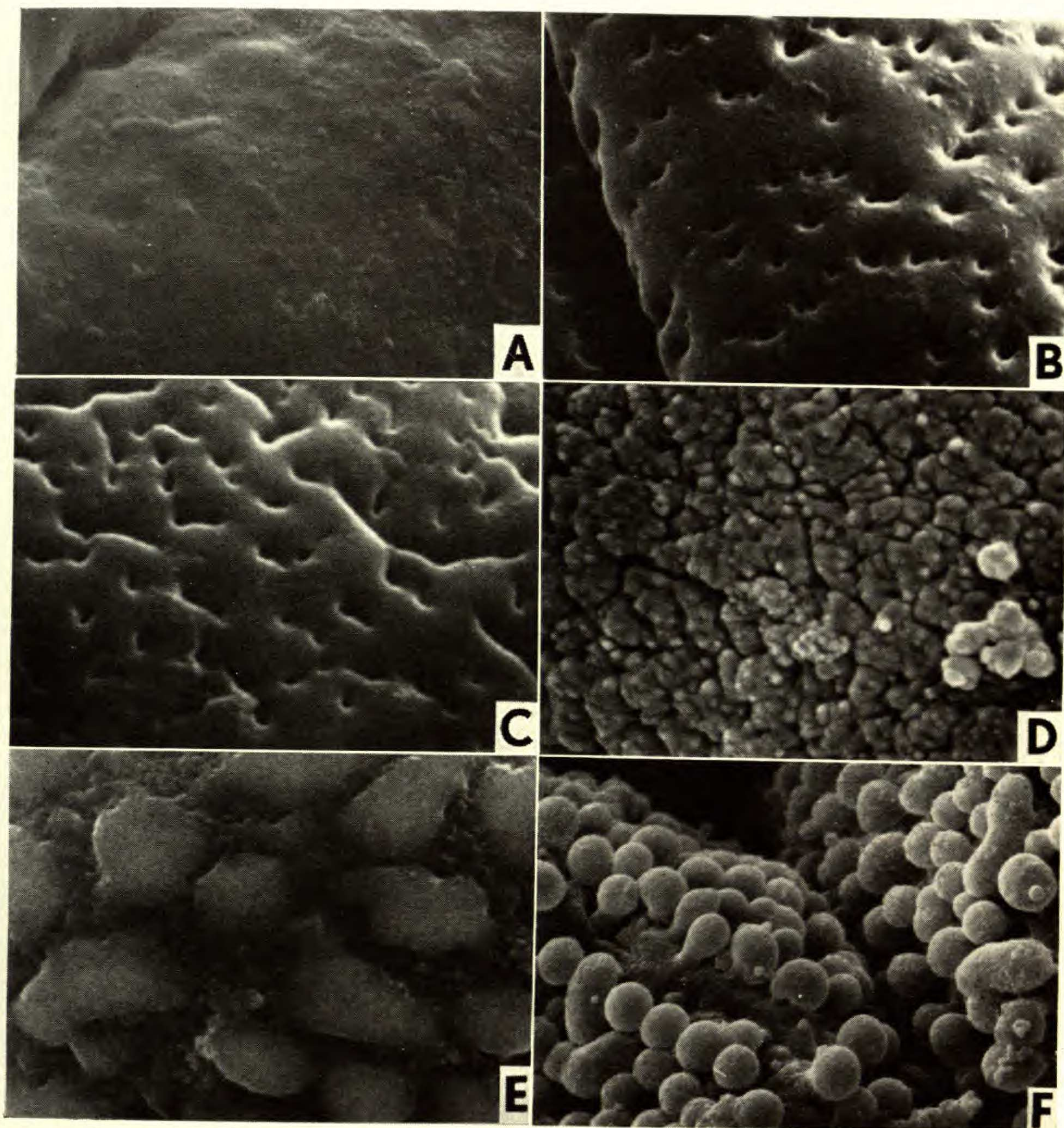


FIGURE 8. Exine sculpturing types.—A. Psilate pollen;  $\times$  ca. 5000 (*Dialyanthera acuminata* Standl.; Myristicaceae).—B. Foveolate pollen;  $\times$  ca. 10,000 (*Magnolia fraseri* Walt.; Magnoliaceae).—C. Fossulate pollen;  $\times$  ca. 10,000 (*Pseudoxandra coriacea* R. E. Fries; Annonaceae). Foveolae present also.—D. Scabrate pollen;  $\times$  ca. 8300 (*Capsicodendron dinisii* (Schw.) Occh.; Canellaceae).—E. Verrucate pollen;  $\times$  ca. 4000 (*Orophea luzonensis* Merr. = *Pseuduvaria* sp.; Annonaceae).—F. Gemmate pollen;  $\times$  ca. 4300 (*Ophrypetalum odoratum* Diels; Annonaceae).

*Exine Structure.*—Pollen of angiosperms may be divided into three basic exine structure types (Fig. 7)—tectate, semitectate, and intectate. The “complete” exine which consists of nexine, columellae, and a roof-like tectum is described as tectate, the columellae and tectum constituting the sexine in such pollen. Tectate pollen grains may be further categorized as either tectate-imperforate (without any holes in the tectum, i.e., tectal perforations) or tectate-perforate (with small holes or tectal perforations). In tectate grains, as mentioned above, the possibility exists for elements to be formed upon the roof or tectum, which then constitute the



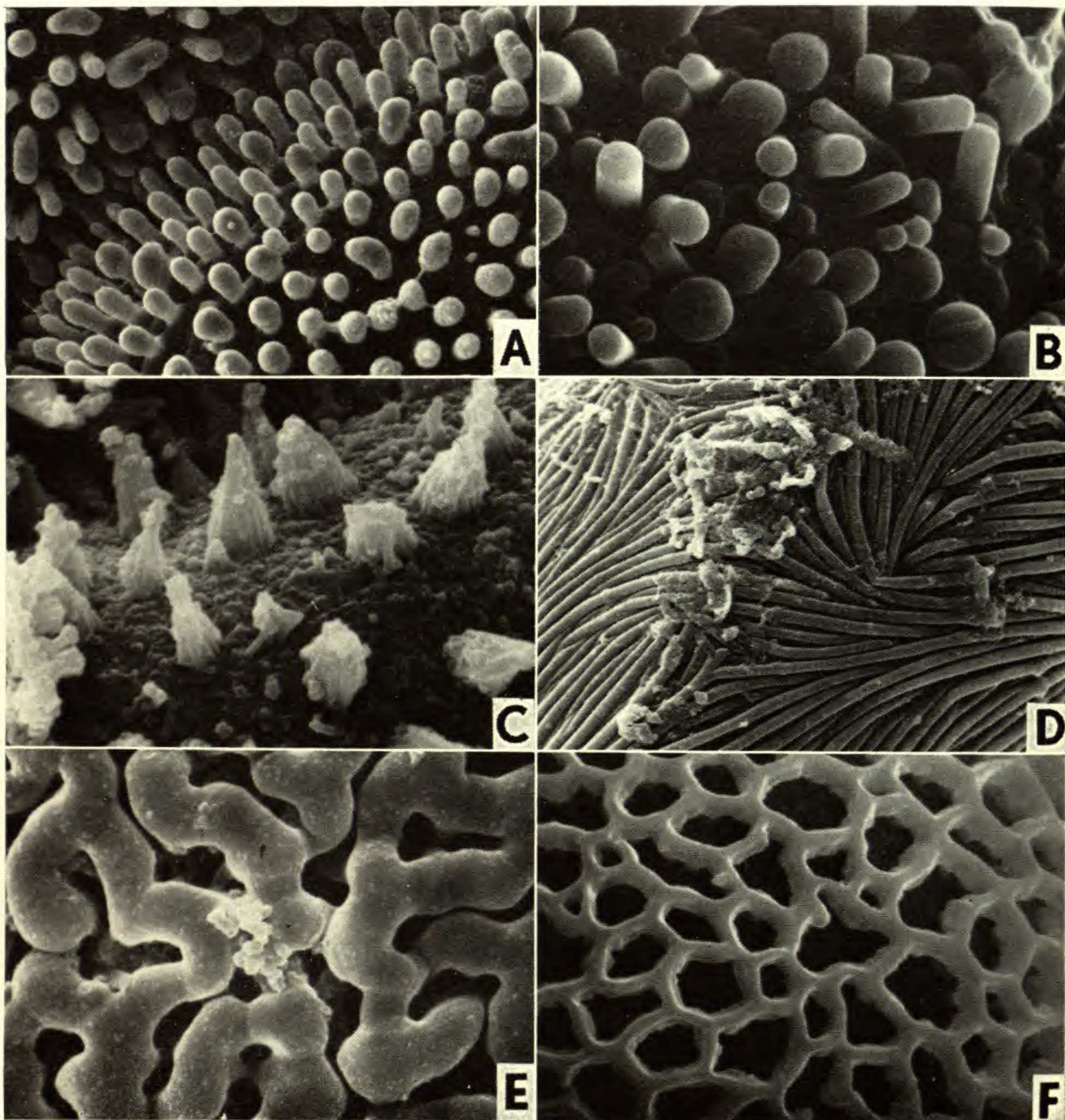


FIGURE 9. Exine sculpturing types.—A. Baculate pollen;  $\times$  ca. 2000 (*Trigynaea caudata* (R. E. Fries) R. E. Fries; Annonaceae).—B. Pilate pollen;  $\times$  ca. 7000 (*Nymphaea candida* J. & C. Presl; Nymphaeaceae). Bacula present also.—C. Echinate pollen;  $\times$  ca. 7400 (*Peumus boldus* Mol.; Monimiaceae).—D. Striate pollen;  $\times$  ca. 3800 (*Cabomba caroliniana* Gray; Cabombaceae).—E. Rugulate pollen;  $\times$  ca. 6500 (*Nelumbo lutea* (Willd.) Pers.; Nelumbonaceae).—F. Reticulate pollen;  $\times$  ca. 4380 (*Saruma henryi* Oliv.; Aristolochiaceae).

sculpturing. Structure in tectate grains is formed by the infratectal columellae which are enclosed by the tectum. Should the tectal perforations in a tectate-perforate exine enlarge so that their diameter becomes greater than the breadth of the pollen wall between them, an open network or reticulum may result composed of the remains of the once complete tectum either held up by otherwise free columellae or lacking columellae, which would constitute the sexine. Such pollen is described as semitectate. In semitectate, reticulate pollen the tectal perforations become spaces or lumina and the walls which make up the reticulum are known as muri. Further, should the tectum be lost entirely and only free, exposed



columellae (or their modified but homologous forms) remain as the sexine, the pollen would be described as intectate. Surface elements present in semitectate and intectate pollen (i.e., the reticulum, the rod-like columellae, etc.) are here defined as comprising *simultaneously* both structure and sculpturing since sculpturing in semitectate and intectate pollen (at least within primitive angiosperms of the subclass Magnoliidae) appears to be homologous with exine structure that previously existed as part of pollen grains which were tectate. In semitectate and intectate pollen the scanning electron microscope may show both structure and sculpturing simply because of this definition. It should also be pointed out that one may observe structure using the scanning electron microscope even in tectate pollen grains if the grains have been broken (cf. Fig. 7D). Finally, it must be mentioned that some magnoliid angiosperms have pollen grains with a morphologically homogeneous exine which appears to be primitively devoid of columellae. Such pollen has been designated "atectate." With reference to sculpturing, tectate pollen may be described as supra-ornate because the sculpturing elements are upon the tectum, while semitectate and intectate pollen may be designated per-ornate because they lack a tectum and their surface ornamentation represents simultaneously structure and sculpturing.

*Exine Sculpturing.*—Exine sculpturing consists of any exposed surface details of the pollen wall. The same sculpturing terms are used in the case of tectate and intectate pollen, with the understanding that the sculpturing in tectate grains is supratectal and distinct from the underlying structure, while sculpturing and structure are synonymous in intectate grains. Semitectate grains by definition are sculptured and are usually reticulate, the reticulum constituting both structure and sculpturing. Major exine sculpturing types (Figs. 8–9) include the following: (1) psilate (smooth); (2) foveolate (pitted); (3) fossulate (grooved); (4) scabrate (with very fine projections, usually defined as less than  $1\mu$ ); (5) verrucate (warty); (6) baculate (with rod-like sculpturing elements); (7) pilate (with pila, i.e., rod-like sculpturing elements with swollen heads; synonym: clavate<sup>7</sup>); (8) gemmate (with sessile pila); (9) echinate (spiny); (10) rugulate (with elongate sculpturing elements irregularly distributed tangentially over the pollen surface); (11) striate (with elongate, more or less parallel sculpturing elements distributed tangentially over the pollen surface); and (12) reticulate (with sculpturing elements forming an open network or reticulum over the pollen surface). Should the sculpturing elements be supra-tectal (i.e., the pollen is supra-ornate), the prefix supra- may be used before the sculpturing type, e.g., supra-verrucate, supra-baculate, supra-echinate, etc. Sculpturing in per-ornate pollen lacking a tectum may be designated by use of the prefix per- before the sculpturing type, e.g., per-verrucate, per-baculate, per-echinate, etc.

*Evolution of Pollen Wall Architecture.*—Evolutionary trends in pollen wall architecture offer great potential as sources of phylogenetic information of major importance. However, to date most studies have not attempted to examine wall architecture with specific evolutionary goals in mind, but have rather concentrated on descriptive or developmental aspects of a number of usually unrelated taxa.

<sup>7</sup> Should the pila be arranged in a reticulate pattern but not actually united into a true reticulum, the grains may be described as retipilate.



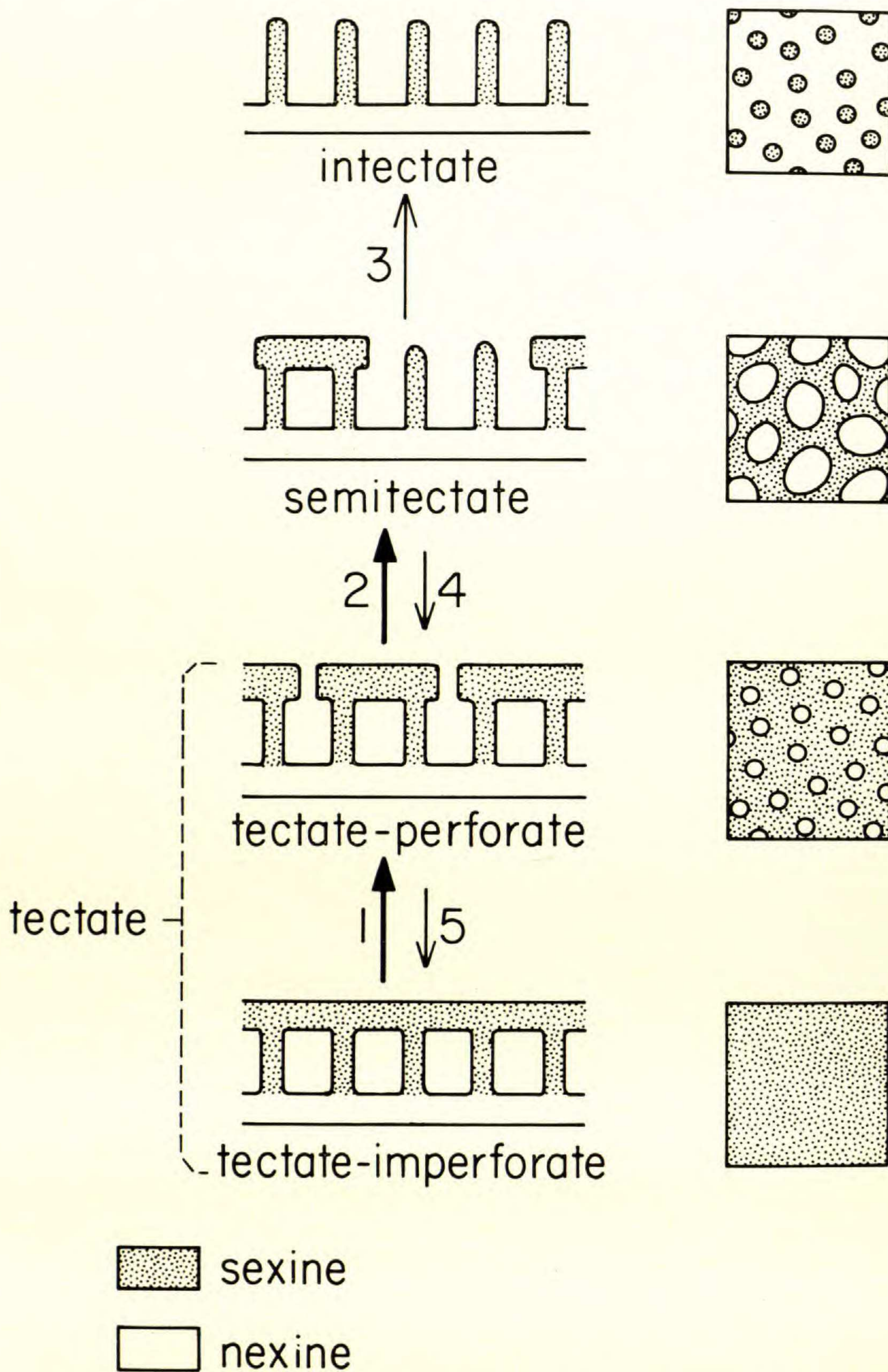


FIGURE 10. Evolutionary trends in angiosperm exine structure types. Cross-sectional views to the left, surface views to the right. Strong arrows 1 and 2 indicate more common stages; weaker arrow 3 indicates less frequently observed stage. Arrows 4 and 5 indicate possible reversibility of the trend, particularly in its earlier stages. The most primitive atectate type of exine structure is not shown.



More comparative studies on the nature of the pollen wall in related groups of plants are required to realize the full phylogenetic potential of pollen wall morphology. Studies presently available, however, appear to reveal the following general evolutionary trends. The pollen wall in most angiosperms consists of both intine and exine. Reduced pollen with little or no exine, as often observed in aquatic angiosperms, clearly represents an advanced condition. Studies in progress on ranalean pollen suggest that a great amount of phylogenetic information resides in the stratification of the exine itself. Preliminary investigations (Walker & Kemp, 1972) have shown that the ratio of nexine to sexine is phylogenetically important. Current studies indicate that presence or absence of endexine and foot-layers, as well as their thickness relative to other layers of the pollen wall, are also phylogenetically useful characters. However, current data are insufficient to allow generalizations of major evolutionary trends in exine stratification at this time. Study of primitive angiosperm families of the subclass Magnoliidae has revealed that some extant angiosperms possess atectate pollen, primitively devoid of columellae (Walker, 1974a; Walker & Skvarla, 1975). From such pollen, a major evolutionary trend in angiosperm exine structure appears to run from pollen which is tectate-imperforate to tectate-perforate and semitectate pollen, and thence more rarely to intectate pollen (Fig. 10; Walker, 1974b). Thus, it appears that sculpturing in angiosperm pollen was primitively supra-ornate, later per-ornate. With reference to exine sculpturing types, primitive angiosperm pollen appears to have been more or less psilate (Walker, 1975), although sculpturing itself undoubtedly represents a more or less reversible character which must be interpreted in terms of individual correlations observed within any given taxa. For more detailed discussions, see Walker (1976).

#### POLLEN-UNIT

The pollen-unit (Walker, 1971b) is the grouping in which pollen is found at maturity within the anther locules of the stamen. Most pollen at maturity consists of solitary grains or monads (Fig. 11A). However, some or all members of approximately 55 families of angiosperms (representing 43 dicot and 12 monocot families) have mature pollen grains in pollen-units other than monads, i.e., in dyads, tetrads, pseudomonads (cryptotetrads), polyads, massulae, or pollinia (Table 2).

*Dyads*.—The regular production of dyads which consist of two pollen grains held together as a unit is rather infrequent, and occurs chiefly in the two families Podostemaceae and Scheuchzeriaceae.

*Tetrads (Including Pseudomonads or Cryptotetrads)*.—The most common pollen-unit other than monads is the tetrad, which represents a retention of the four products resulting from meiosis of the pollen mother cell. However, in connection with some pollen characters, e.g., particularly pollen grain shape, a clear distinction must be made between the cytological-embryological meiotic tetrad and the mature pollen tetrad of the palynologist. Tetrads may be classified into tetrad types (Fig. 12) according to the spatial arrangement of the individual pollen grains within the tetrad. In this regard, there are two fundamentally different types of pollen tetrads—uniplanar with all grains (and particularly their



TABLE 2. Angiosperm families with pollen-units other than monads.<sup>a</sup>

| DICOTYLEDONS                    |                                                          |
|---------------------------------|----------------------------------------------------------|
| Magnoliidae                     | +++Ericaceae                                             |
| +++Lactoridaceae                | ++Epacridaceae                                           |
| +++Winteraceae                  | +++Empetraceae                                           |
| ++Annonaceae (also polyads)     | +++Pyrolaceae                                            |
| Monimiaceae                     |                                                          |
| Nymphaeaceae                    | Rosidae                                                  |
|                                 | Saxifragaceae                                            |
| Ranunculidae                    | Rosaceae                                                 |
| Berberidaceae                   | ++Leguminosae (also polyads)                             |
| Papaveraceae                    | ++Podostemaceae (dyads, possibly polyads)                |
|                                 | +Onagraceae                                              |
| Caryophyllidae                  | Cornaceae                                                |
| Didiereaceae (possibly tetrads) | Rafflesiaceae                                            |
|                                 | +Hippocrateaceae (also polyads)                          |
| Hamamelididae                   | Celastraceae (also polyads)                              |
| +++Myrothamnaceae               | Sapindaceae                                              |
| Eucommiaceae                    |                                                          |
|                                 | Asteridae                                                |
| Dilleniidae                     | ++Gentianaceae (also polyads)                            |
| +++Sarcolaenaceae               | ++Apocynaceae                                            |
| Actinidiaceae                   | +++Asclepiadaceae (also polyads, massulae, and pollinia) |
| Guttiferae                      | Solanaceae                                               |
| Tiliaceae                       | +Bignoniaceae                                            |
| Lecythidaceae                   | Pedaliaceae                                              |
| +++Nepenthaceae                 | +++Hydrostachyaceae                                      |
| +++Droseraceae                  | Goodeniaceae                                             |
| Begoniaceae                     | +Rubiaceae                                               |
| Datiscaceae                     |                                                          |
| Cucurbitaceae                   |                                                          |
| MONOCOTYLEDONS                  |                                                          |
| Alismatidae                     | +++Orchidaceae (also polyads, massulae, and pollinia)    |
| Hydrocharitaceae                |                                                          |
| +++Scheuchzeriaceae (dyads)     |                                                          |
|                                 | Commelinidae                                             |
| Arecidae                        | +++Juncaceae                                             |
| Araceae                         | +++Thurniaceae                                           |
|                                 | +++Cyperaceae (pseudomonads or cryptotetrads)            |
| Liliidae                        | +++Typhaceae                                             |
| Philydraceae                    | Bromeliaceae                                             |
| Liliaceae (~ Amaryllidaceae)    |                                                          |
| ++Velloziaceae                  |                                                          |

<sup>a</sup> Based mostly on data of Erdtman (1945b, 1966); tetrads present unless otherwise stated. The symbols in front of families indicate that tetrads or other pollen-units larger than monads occur respectively in all members or the overwhelming majority of the family (+++), in a significant number of genera in the family (++), or in several genera in the family (+). No symbols before a family indicates that pollen-units other than monads are very rare in the family or may only be found in certain individual plants of a species (e.g., pollen tetrads found in material from one particular tree of *Eucommia*).

polar axes) in the same plane and multiplanar with grains (and their polar axes) in more than one plane. Uniplanar tetrads may be tetragonal (square, isobilateral; Fig. 11C), rhomboidal (Fig. 11D), linear, or T-shaped, while multiplanar tetrads may be tetrahedral (Fig. 11E) or decussate (cross-shaped; Fig. 11F). As a rule, the monosulcate pollen of magnoliid dicots and monocots occurs in tetragonal tetrads, while the tricolpate pollen of the non-magnoliid dicotyledons is generally found in tetrahedral tetrads.



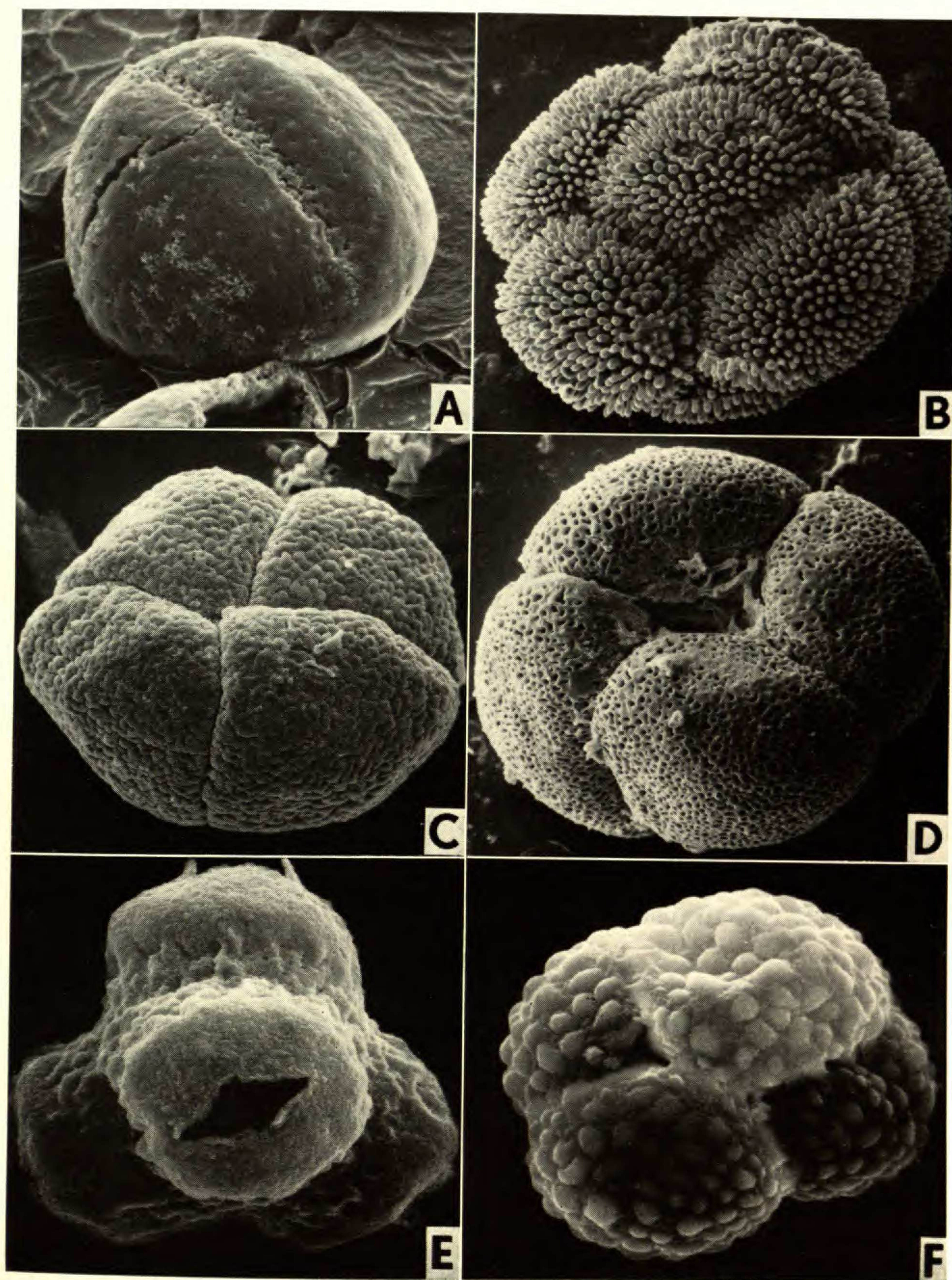
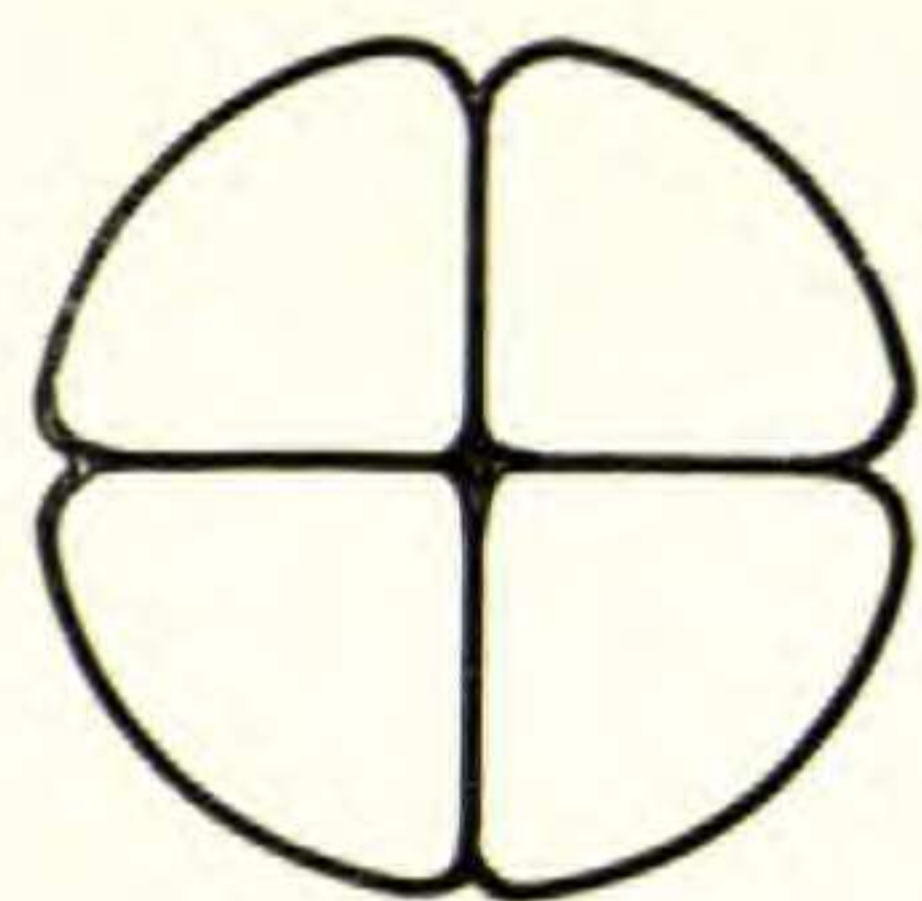


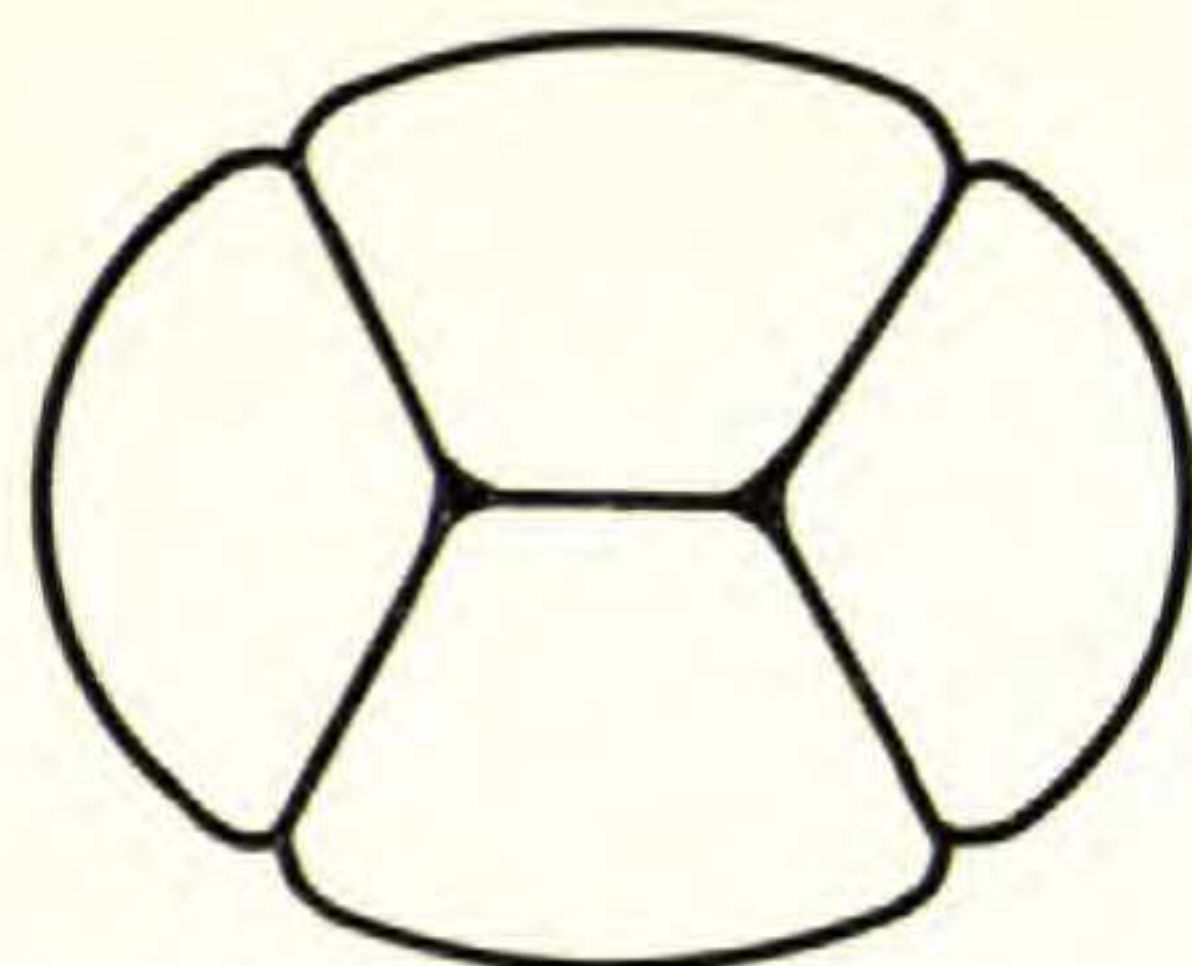
FIGURE 11. Types of pollen-units.—A. Monad;  $\times$  ca. 1840 (*Warburgia ugandensis* Sprague; Canellaceae).—B. Polyad (octad);  $\times$  ca. 700 (*Trigynaea caudata* (R. E. Fries) R. E. Fries; Annonaceae).—C. Tetragonal tetrad;  $\times$  ca. 970 (*Uvariastrum hexaloboides* (R. E. Fries) R. E. Fries; Annonaceae).—D. Rhomboidal tetrad;  $\times$  ca. 375 (*Annona muricata* L.; Annonaceae).—E. Tetrahedral tetrad;  $\times$  ca. 1500 (*Lactoris fernandeziana* Phil.; Lactoridaceae).—F. Decussate tetrad;  $\times$  ca. 1050 (*Orophea luzonensis* Merr. = *Pseuduvaria* sp.; Annonaceae).



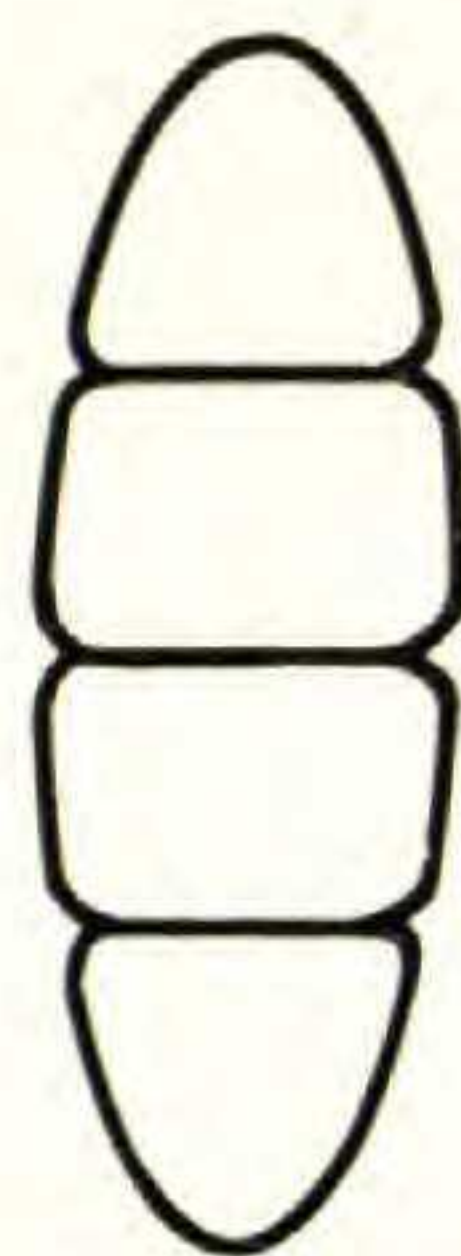
## UNIPLANAR



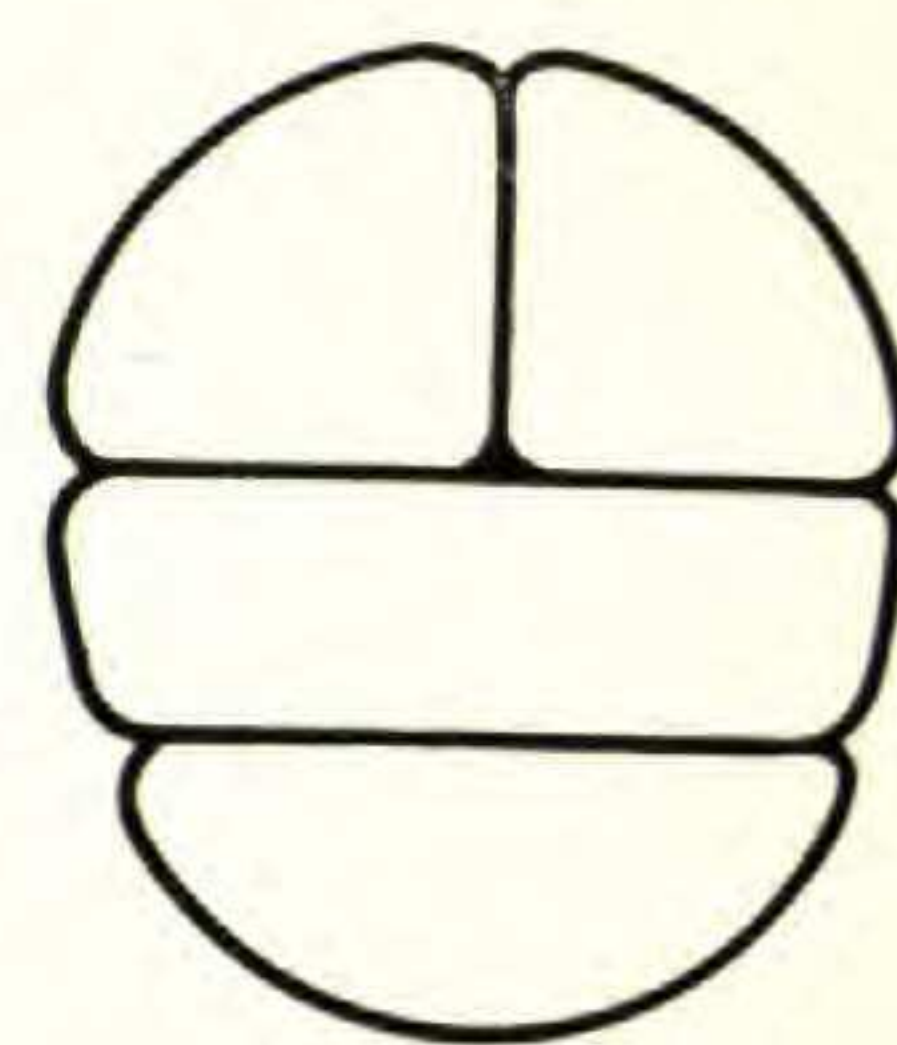
tetragonal



rhomboidal

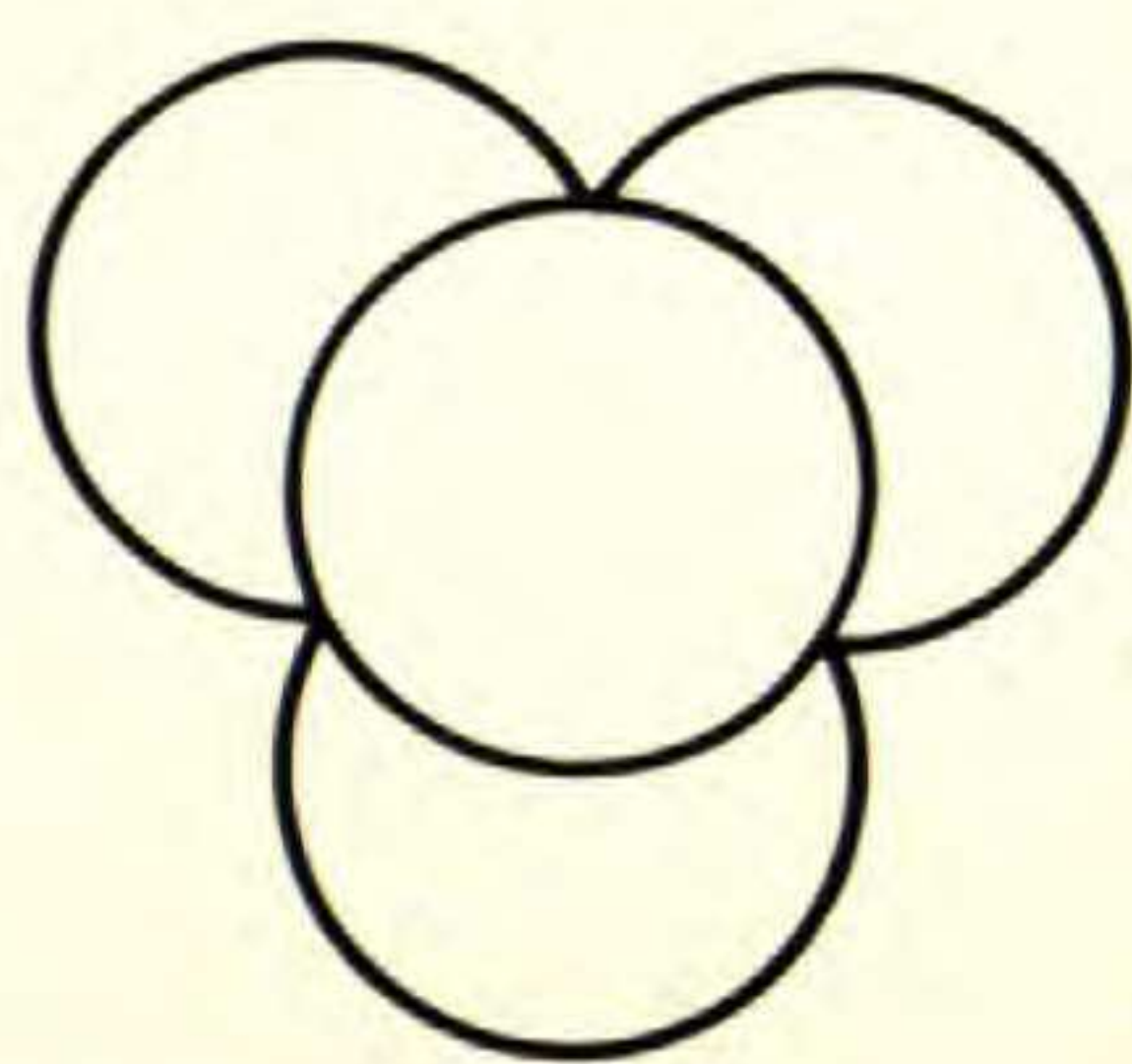


linear

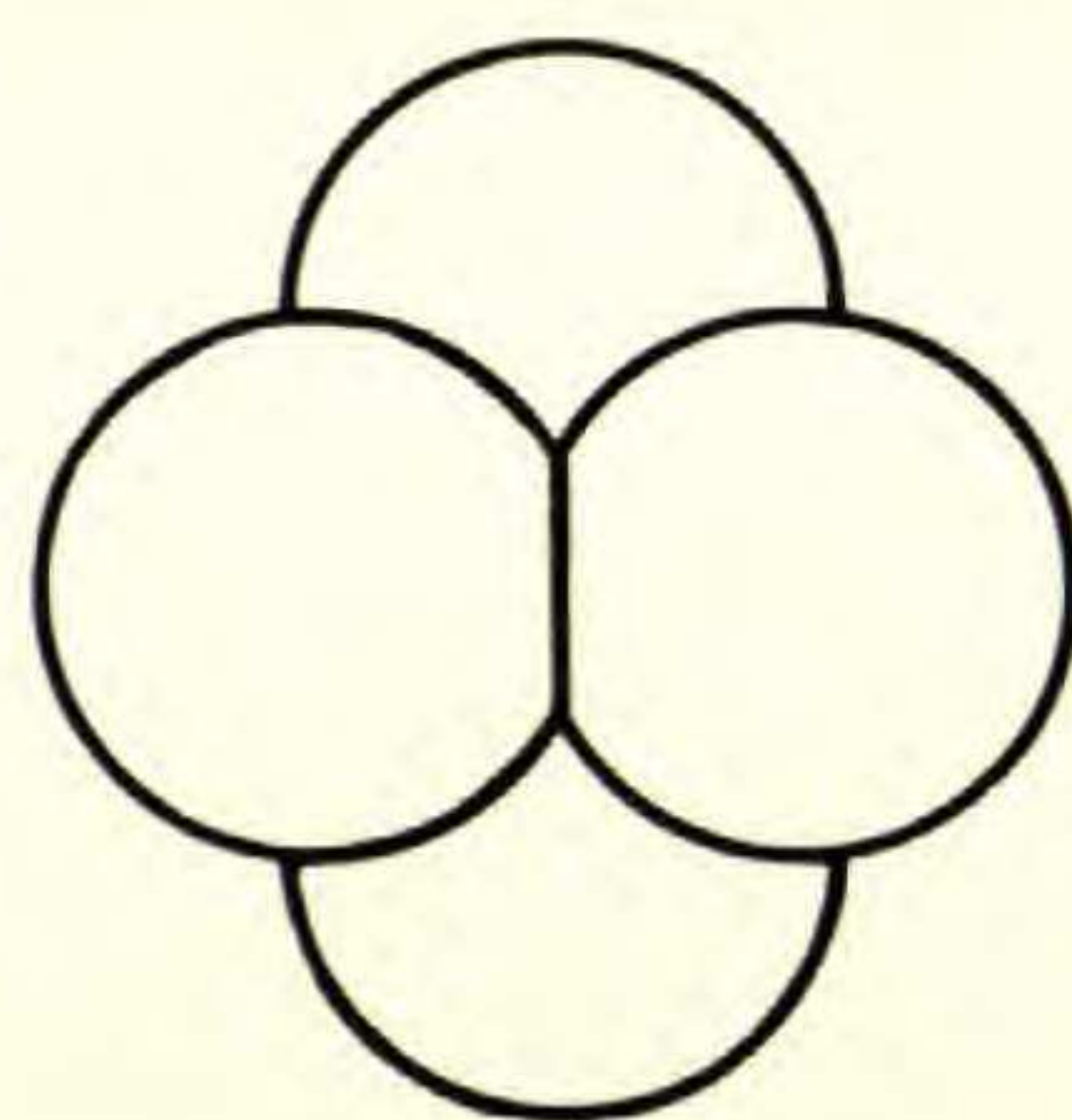


T-shaped

## MULTIPLANAR



tetrahedral



decussate

FIGURE 12. Pollen tetrad types. See text for discussion.

Of the approximately 50 angiosperm families with pollen in tetrads (Table 2), 13 have their pollen grains entirely or almost entirely in tetrads, six have a significant number of genera with some or all species with tetrads, four have several genera with pollen in tetrads, and the remainder (27 families) have tetrads only rarely. The Cyperaceae have pseudomonads (cryptotetrads) which are morphological monads that are actually homologous to tetrads since in this family the wall of the apparent solitary pollen grain is actually formed by the pollen mother cell that contains a pollen tetrad in which three of the four grains fail to develop.

*Polyads*.—Polyads (Fig. 11B), which are pollen-units of a definite number greater than four, e.g., octads, 16's, etc.,<sup>8</sup> are much less common than tetrads and have been reported only in the following seven angiosperm families: Annonaceae, Leguminosae (Mimosoideae), Hippocrateaceae, Celastraceae, Gentianaceae,

<sup>8</sup> At least two polyads or massulae must occur in each anther locule, otherwise by definition a pollinium, not a polyad or massula, is present.



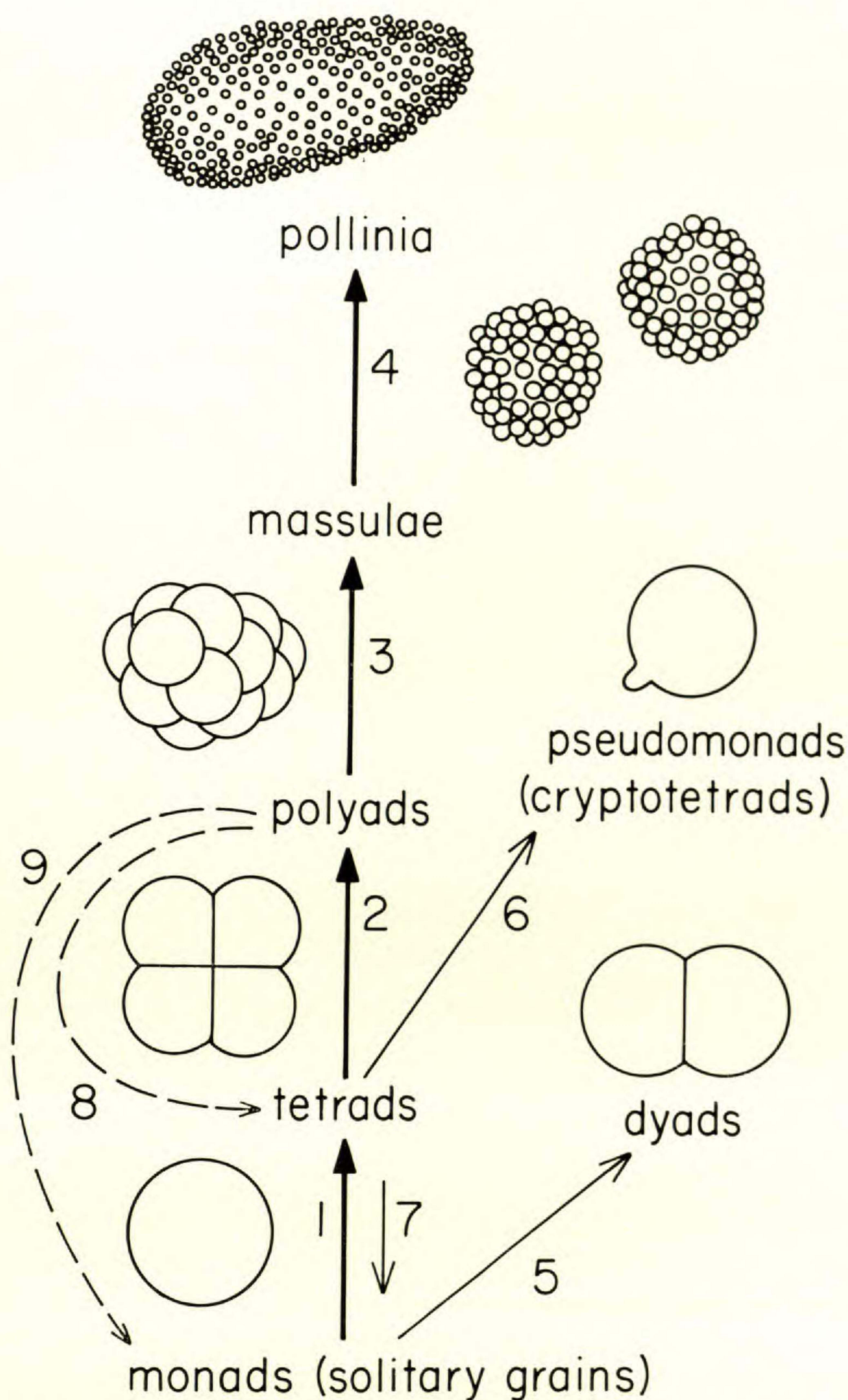


FIGURE 13. Evolutionary trends in angiosperm pollen-units. See text for discussion.

Asclepiadaceae, and Orchidaceae. Polyads may consist of connate but individually discernible tetrads, or they may be more or less irregular with no individual tetrads visible.

*Massulae*.—Massulae are pollen-units that are usually larger than polyads in which the number of individual pollen grains is not ascertainable due to a large



number of grains and/or a large amount of pollen fusion.<sup>8</sup> The Asclepiadaceae and Orchidaceae are the only two families with massulae.

*Pollinia*.—A pollinium consists of the entire pollen-mass of one or more anther locules fused together as a unit. Pollinia, like massulae, are restricted to the families Asclepiadaceae and Orchidaceae.

*Evolution of Pollen-Units*.—Monads clearly represent the basic angiosperm pollen-unit. Regularly occurring, permanent dyads have independently evolved from monads in two families (one dicotyledonous and the other monocotyledonous). Regularly produced permanent tetrads have evolved separately in a number of lines, and represent an advanced character over solitary grains. In some instances, however, monads may have secondarily evolved from tetrads (Walker, 1971b), and in such cases solitary grains represent an advanced rather than a primitive character-state. Pseudomonads (cryptotetrads) apparently have evolved from permanent tetrads since the only family that has pseudomonads (the Cyperaceae) appears to be related to the more primitive family Juncaceae which has permanent tetrads. Polyads occur much less frequently than tetrads but have also evolved independently a number of times. Since in every family that has polyads, some taxa (often clearly the more primitive) possess tetrads, it seems evident that polyads have arisen from tetrads. Also, as previously mentioned, some polyads consist of individually discernible tetrads. Normally polyads represent a more advanced grade than tetrads, but it should not be overlooked that in some lines polyads may have given rise secondarily to tetrads or even to monads. Massulae and pollinia represent the most advanced pollen-units and occur only in two families of angiosperms. Interestingly, both of these families (Asclepiadaceae and Orchidaceae) have tetrads and polyads in their more primitive members. Figure 13 outlines evolutionary trends in angiosperm pollen-units.

#### POLLEN GRAIN POLARITY

Polarity is a quality inherent in a body that has opposite parts or poles, and which as a consequence has one main axis of symmetry. Pollen grain polarity is undoubtedly due to the fact that all pollen results from meiosis of pollen mother cells and thus all pollen grains are at one time or another united together as members of a meiotic pollen tetrad. Individual pollen grains may thus be likened to a globe with poles and an equator (cf. section above, POLLEN APERTURES). The polar axis of a pollen grain, which may also be termed the main or vertical axis, is generally also an axis of symmetry, and in globe-shaped (as opposed to boat-shaped) pollen grains usually an axis of rotation as well. The equatorial plane of a pollen grain perpendicularly bisects the polar axis. The part of the equatorial plane enclosed by the equator of the pollen grain may be called the equatorial outline. The equatorial plane contains two or more horizontal symmetry axes which are known as the equatorial axes. Horizontal symmetry axes (equatorial axes) are the lines which represent the intersection of any vertical planes of symmetry that a particular pollen grain may have with the equatorial plane, such vertical planes of symmetry going through the vertical symmetry axis or polar axis of the pollen grain (cf. section below, POLLEN GRAIN SYMMETRY). For example, monosulcate pollen grains have two equatorial axes which are mutually perpen-



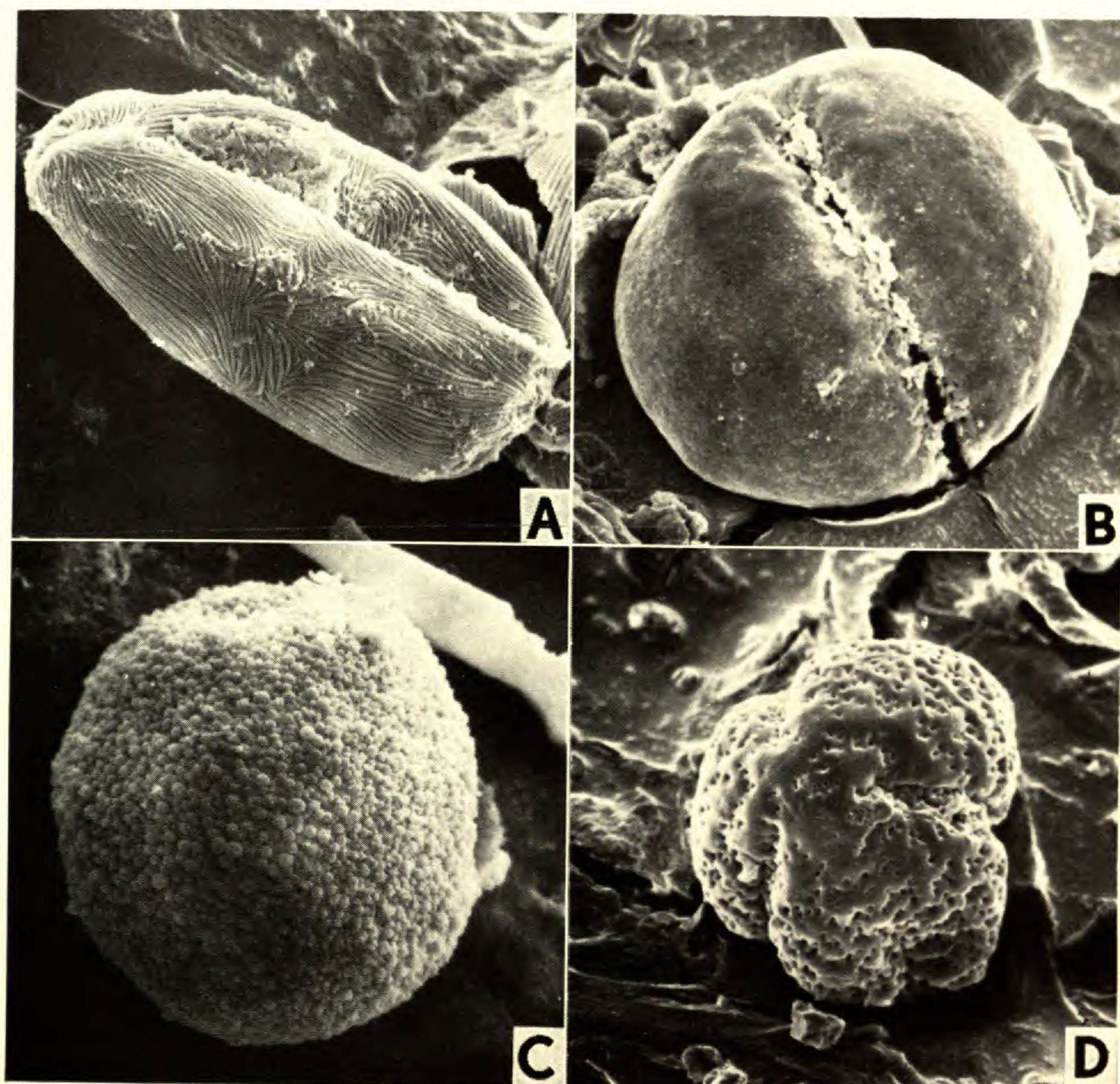


FIGURE 14. Types of pollen grain polarity and symmetry.—A. Heteropolar, bilateral (monosulcate) pollen (*Cabomba caroliniana* Gray; Cabombaceae). Equatorial view;  $\times$  ca. 1370.—B. Heteropolar, isobilateral (monosulcate) pollen (*Dialyanthera otoa* (Humb. & Bonpl.) Warb.; Myristicaceae). Presumed distal-polar view;  $\times$  ca. 1500.—C. Apolar, radiosymmetric (inaperturate) pollen (*Xymalos monospora* (Harv.) Baill.; Monimiaceae);  $\times$  ca. 2810.—D. Isopolar, radiosymmetric (tricolpate) pollen (*Lardizabala biternata* Ruiz & Pav.; Lardizabalaceae). Polar view;  $\times$  ca. 1460.

dicular, inaperturate pollen has an infinite number of equatorial axes, dicolpate, diporate, and disulculate pollen grains have two mutually perpendicular equatorial axes, and tricolpate and triporate pollen has three equatorial axes, none of which is perpendicular to each other. It must be emphasized that there is a fundamental difference between the polar axis and an equatorial axis in that there is only one polar axis (vertical symmetry axis) while there are always at least two, sometimes (in the case of inaperturate pollen) even an infinite number of equatorial axes (horizontal symmetry axes).

Pollen grains may be without distinct polarity and apolar (Fig. 14C), i.e., without discernible poles once the grains have separated from the meiotic pollen tetrad, or pollen may be polar with recognizable poles even after the grains have



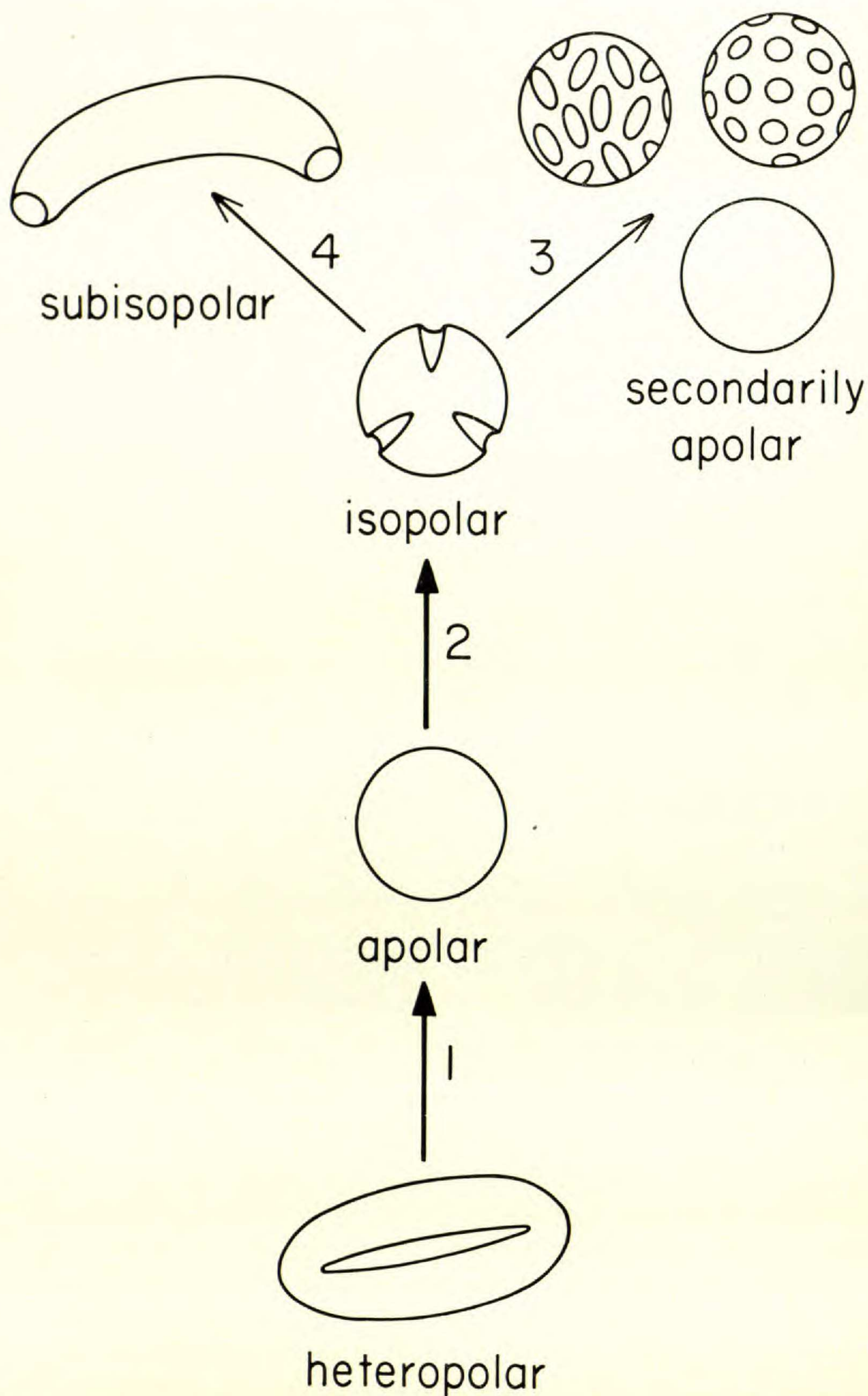


FIGURE 15. Major evolutionary trends in the polarity of angiosperm pollen. Heteropolar and isopolar pollen shown in polar view; subisopolar pollen shown in more or less equatorial view. See text for discussion.



separated from the pollen tetrad. Pollen that at first appearance seems to be apolar, but which upon closer examination proves to possess a more or less distinct polarity may be designated cryptopolar. Polar pollen grains may be further characterized as isopolar (Fig. 14D), with the equatorial plane dividing the grain into similar halves, or heteropolar (Figs. 14A, B), with the polar faces markedly dissimilar. Grains which usually have a more or less curved equatorial plane and possess only slight differences between the distal and proximal faces (e.g., one face may be very convex, the other less convex, plane, or even concave) may be termed subisopolar.

Pollen grain polarity is of two types—apparent and absolute. Apparent polarity is usually due to the aperture(s) present and/or to possession of a distinct vertical axis of symmetry, which usually appears as an axis of rotation also. Less frequently, apparent polarity may be related to exine sculpturing, either alone or in conjunction with apertures and/or a vertical axis of symmetry-rotation. Apparent pollen grain polarity is usually the same as absolute polarity, but it is essential for clear palynological thinking to keep the distinction between apparent and absolute pollen grain polarity in mind. The former is based on indirect but normally reliable clues observed in solitary pollen grains (apertures, sculpturing, a vertical axis of symmetry-rotation), while the latter is based on direct observation of pollen tetrads. In the majority of cases absolute pollen polarity must be inferred from apparent pollen polarity since most pollen is shed in the form of monads.

*Evolution of Pollen Grain Polarity.*—Major evolutionary trends in the polarity of angiosperm pollen are outlined in Fig. 15. Since polarity is largely determined by aperture condition, the primitive type of angiosperm pollen grain polarity (heteropolarity) is directly related to possession of a monosulcate pollen aperture. From such heteropolar pollen the main evolutionary trend has been to apolar inaperturate grains, and from pollen of this type to the basic isopolar colpate pollen of non-magnoliid dicotyledons.<sup>9</sup> Apolar inaperturate, rugate, and forate pollen has been derived secondarily from isopolar colpate pollen within some non-magnoliid dicotyledons. In other non-magnoliid dicots, isopolar pollen grains have given rise to subisopolar pollen. Evolutionary trends in spore as well as pollen grain polarity have been discussed by Chaloner (1970).

#### POLLEN GRAIN SYMMETRY

Symmetry is the quality inherent in a body which is capable of division into similar or equal halves (i.e., mirror images). Pollen grain symmetry is the correspondence on opposite sides of a median plane in the size and shape of the resulting halves, and similarly in the number, relative position, and type of pollen apertures present. Such median planes are known as symmetry planes. In addition, pollen grains may have symmetry axes. Symmetry axes are lines which run through the center of the pollen grain and either go through both poles (the vertical symmetry axis or polar axis) or lie in the equatorial plane and represent the intersection of all vertical planes of symmetry with the equatorial plane

<sup>9</sup> A minor trend from heteropolar, anasulcate pollen directly to isopolar, zonizonasulcate pollen via an anazonasulcate intermediary without an apolar, inaperturate intermediate stage may be observed within the pollen of the family Nymphaeaceae.



TABLE 3. Number of symmetry axes and planes in different types of pollen grains.

| Pollen Type                                                                | Vertical Axes<br>(polar axis) | Vertical Planes<br>(polar planes)                          | Horizontal Axes<br>(equatorial axes)                       | Horizontal Planes<br>(equatorial plane) |
|----------------------------------------------------------------------------|-------------------------------|------------------------------------------------------------|------------------------------------------------------------|-----------------------------------------|
| Heteropolar,<br>monosulcate<br>pollen                                      | 1                             | 2                                                          | 2                                                          | 0                                       |
| Apolar,<br>inaperturate<br>pollen                                          | 1                             | $\infty$                                                   | $\infty$                                                   | 1                                       |
| Isopolar pollen<br>with 2-many,<br>equidistant,<br>equatorial<br>apertures | 1                             | Same number<br>as equatorial<br>apertures,<br>i.e., 2-many | Same number<br>as equatorial<br>apertures,<br>i.e., 2-many | 1                                       |
| Total Range                                                                | 1                             | 2- $\infty$                                                | 2- $\infty$                                                | 0-1                                     |

of the pollen grain (horizontal symmetry axes or equatorial axes), such vertical planes of symmetry going through the vertical symmetry axis (polar axis) of the pollen grain. Thus, symmetry axes and planes may be either vertical or horizontal, depending on whether they go through the poles or the equator of the pollen grain. Pollen grains have only one vertical *axis* of symmetry (the polar or main axis), while there may be from two to an infinite number of vertical *planes* of symmetry (i.e., polar symmetry planes). On the other hand, there may be one or no horizontal planes of symmetry (i.e., equatorial symmetry planes), while there are always at least two and sometimes an infinite number of horizontal axes of symmetry (i.e., equatorial axes). In any given pollen grain the number of equatorial axes always equals the number of vertical planes of symmetry. Horizontal symmetry axes and vertical symmetry planes always go through the polar axis. Horizontal symmetry axes perpendicularly bisect the polar axis, and like vertical symmetry planes they may be mutually perpendicular. By definition, pollen grain symmetry is based on the planes of symmetry that exist in a particular grain *as seen from polar view*, i.e., on vertical, not horizontal, symmetry planes.<sup>10</sup> With reference to three common types of pollen grains, the number of vertical symmetry planes are as follows: two in heteropolar, monosulcate grains; infinite in apolar, inaperturate grains; and the same as the number of apertures in isopolar grains with equatorial apertures that are equidistant. On the other hand, all heteropolar pollen grains would have no horizontal symmetry planes, while both apolar inaperturate grains and isopolar grains with two or more equidistant equatorial apertures would have one horizontal symmetry plane (cf. Table 3).

Pollen grain symmetry is largely determined by grain shape and apertures.

<sup>10</sup> For the purpose of symmetry determination heteropolar grains must be observed from the pole which possesses the aperture(s). If both poles should possess apertures and they are dissimilar in shape, number, or position from one pole to the other, then the grain could have two different types of symmetry depending on the pole observed. In such cases the two symmetry types should be recorded with respect to occurrence on either the distal or proximal pole, if possible.



Symmetry as applied to pollen grains is based on (1) the number of vertical planes of symmetry that exist in a particular grain, (2) whether the equatorial axes of the grain are all of equal length or not, i.e., generally whether the equatorial outline is circular or not, and (3) the nature of the aperture(s) present. Rarely, pollen may be more or less asymmetric due to irregular grain shape resulting from occurrence of random protuberances of the exine, i.e., protuberances of the outer pollen wall itself, not merely localized variation in surface sculpturing elements, or because of the unsymmetrical distribution of apertures preventing a division into similar halves. Symmetric pollen grains, which are capable of division into similar halves, may be further classified as radiosymmetric or bisymmetric. Radiosymmetric pollen (Figs. 14C, D) is divisible into equal symmetrical portions by any of three or more (up to infinity) equidistant vertical planes of symmetry passing through the polar axis, i.e., all three or more equatorial axes are equidistant. Bisymmetric grains are doubly symmetrical, i.e., divisible into two similar halves by either of two (never three or more) mutually perpendicular vertical planes of symmetry passing through the polar axis. Bisymmetric pollen may be either bilateral or isobisymmetric. Bilateral<sup>11</sup> pollen grains (Fig. 14A) have two mutually perpendicular vertical planes of symmetry passing through the polar axis which are of different length, i.e., the two equatorial axes are not equidistant and the equatorial outline of the grain is elliptical, oval, etc., but not circular. Isobisymmetric grains<sup>12</sup> have two mutually perpendicular vertical planes of symmetry passing through the polar axis which are the same length, i.e., the two equatorial axes are equidistant and the equatorial outline of the grain is usually more or less circular. Isobisymmetric pollen may be either isobilateral or biradial. Isobilateral pollen grains (Fig. 14B) are isobisymmetric grains that are heteropolar and monosulcate, their isobisymmetry being a function largely of the elongate nature of their polar aperture. They are essentially bilateral pollen grains with a round rather than elongate equatorial outline. Biradial pollen is also isobisymmetric, but biradial grains are isopolar and equatorially di-aperturate (i.e., either disulcate-diulcate or dicolpate-diporate), their isobisymmetry being chiefly a function of their aperture number (two). They are essentially radial pollen with two rather than three or more apertures.

*Evolution of Pollen Grain Symmetry.*—Major evolutionary trends relating to pollen grain symmetry in angiosperms are outlined in Fig. 16. Primitive boat-shaped, monosulcate pollen has bilateral symmetry. From this primitive type of symmetry the common radiosymmetry of the majority of dicotyledonous pollen

<sup>11</sup> Pollen which is boat-shaped, heteropolar, and monosulcate (or elongate, isopolar, and equatorially di-aperturate, e.g., dicolpate, diporate, disulcate, etc.) has been incorrectly described almost universally by palynologists as bilateral. Bilaterally symmetrical objects are divisible by only a single plane (i.e., are monosymmetric), not two, as are boat-shaped, bisymmetric, monosulcate pollen grains; pollen of this type is more correctly described as anisobisymmetric. However, the more familiar term bilateral, as defined above, has been retained for use in palynological descriptions with the understanding that mathematically this usage of the term bilateral is incorrect, anisobisymmetric being the more proper term.

<sup>12</sup> Erdtman (1966) improperly considered pollen grains with this type of symmetry as radiosymmetric. Since radiosymmetric objects by definition must have three or more planes of symmetry, pollen of this type has been designated as isobisymmetric.



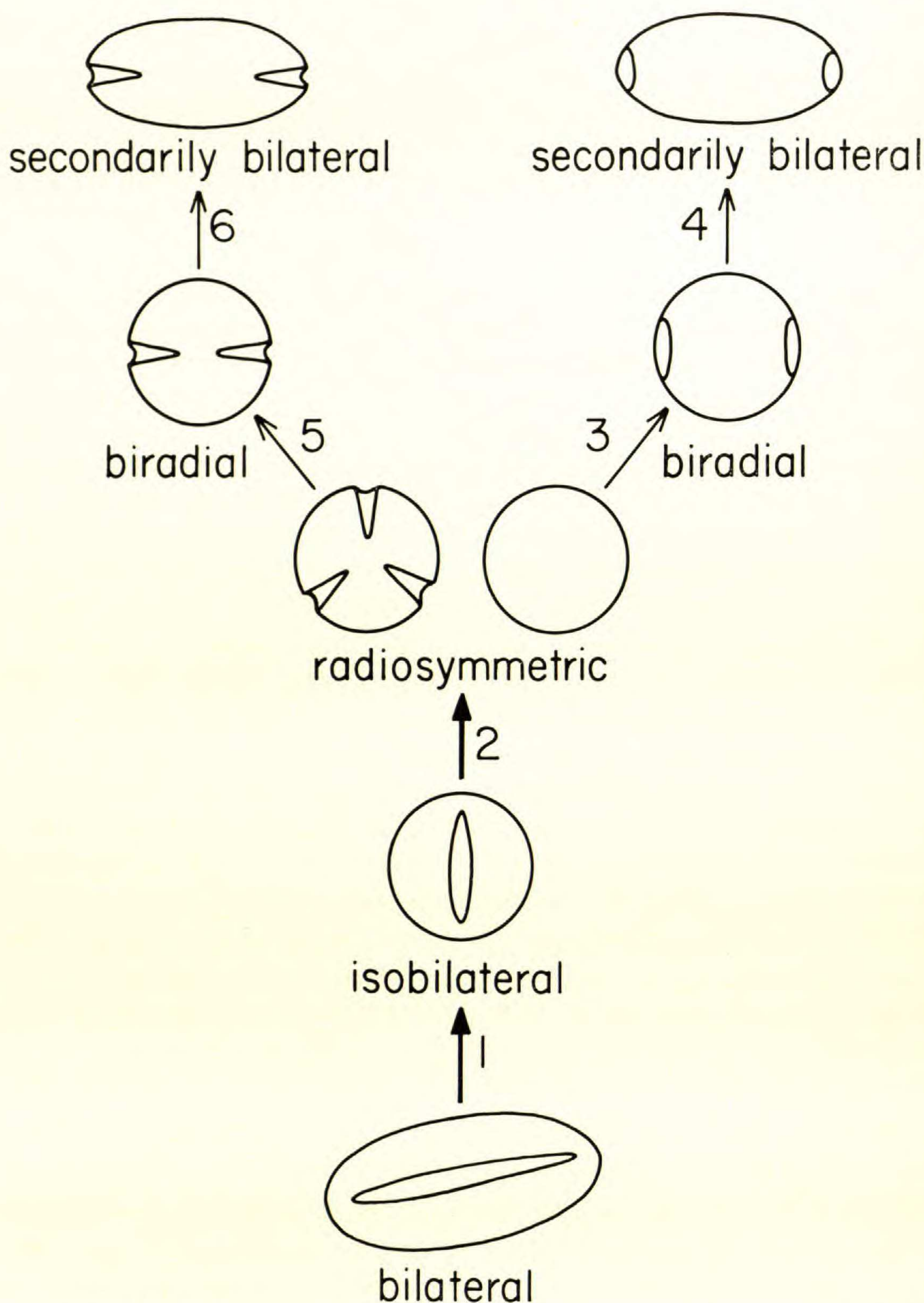


FIGURE 16. Major evolutionary trends in the symmetry of angiosperm pollen. Bilateral, isobilateral, and radiosymmetric tricolpate pollen shown in polar view; biradial and secondarily bilateral pollen all shown in equatorial view. See text for discussion.

has evolved, apparently via an isobilateral intermediate stage which retains a sulcus combined with a circular equatorial outline. Biradial pollen (e.g., dicolpate, diporate, disulculate pollen, etc.) has evolved in a number of families from radially symmetrical grains because of the occurrence of only two apertures. Such biradial pollen may change its shape from spherical to equatorially elongate, thus producing pollen which is secondarily bilateral.



## POLLEN GRAIN SHAPE

Shape is the spatial form of a body. Pollen grain shape is correlated largely with aperture type which in turn is more or less correlated with polarity and symmetry. It should be pointed out that method and length of pollen preparation may cause the shape of pollen grains to vary considerably. With reference to shape, angiosperm pollen may be either nonfixiform (without definite shape) or fixiform (with definite shape). The rare nonfixiform type of pollen occurs in many marine angiosperms such as *Zostera*, in which the pollen, that may be over  $2000\mu$  long, is threadlike. Normal, fixiform angiosperm pollen may be divided into two basic shape classes—boat-shaped and globose (globe-shaped). Boat-shaped pollen (Figs. 17A–C), as the name implies, is boat-like with a short polar axis and one equatorial axis that is longer than the other. Its most prominent axis of rotation coincides with the longer equatorial axis and its polar axis is generally not a prominent axis of rotation. Its equatorial outline is usually more or less elliptical to oblong, and its polarity is due to apertures present, not its symmetry. Boat-shaped pollen may be further divided into a number of subtypes depending on the ratio of the longer equatorial axis to the shorter. If this ratio is greater than 1.00 but less than 1.50, the pollen is boat-shaped-elliptic (Fig. 17C), while pollen with a ratio between 1.50 and 1.99 is boat-shaped-oblong (Fig. 17B). Any pollen grains with a ratio equal to or greater than 2.00 are described as boat-shaped-elongate (Fig. 17A).

Globose pollen (Figs. 17D–F), on the other hand, is basically globe-shaped with its equatorial axes all the same length and its polar axis is generally a prominent axis of rotation. Its equatorial outline is usually more or less circular or some modification thereof such as triangular, lobed, etc., and its polarity generally results from both its symmetry and its apertures. The shape of most globose pollen is that of an ellipsoid with the polar axis as axis of rotation. Globose pollen may also be further subdivided, depending on the ratio of polar to equatorial axes. If both polar and equatorial axes are the same length, the pollen is spherical (Fig. 17D). If the polar axis is shorter than the equatorial axes, i.e., the grains are compressed along the polar axis, the pollen is flattened or oblate (Fig. 17E).<sup>13</sup> And finally, if the polar axis is longer than the equatorial axes, i.e., the grains are compressed around the equator rather than along the polar axis, the pollen is prolate (Fig. 17F).<sup>13</sup> A more comprehensive classification of globose pollen is outlined in Table 4, which is slightly modified from Erdtman (1966). At times, di-aperturate, globose pollen, e.g., disulculate or diporate pollen, may have a more or less elliptical to oblong equatorial outline, with one equatorial axis longer than the other. Globose pollen of this type (which is also secondarily bilateral) is described as globose-elliptic, -oblong, or -elongate, depending on whether the ratio of the longer equatorial axis to the shorter is greater than 1.00 but less than 1.50, is between 1.50 and 1.99, or is equal to or greater than 2.00.

The outline of a pollen grain as seen in polar view with the polar axis directed towards the observer is known as the pollen amb. In most pollen the amb coincides

<sup>13</sup> The terms oblate and prolate are used here in a broader sense than that of Erdtman (1966). It is suggested that Erdtman's oblate and prolate be replaced by the terms *euoblate* and *euprolate*, so that the former may be used as broader grouping terms.



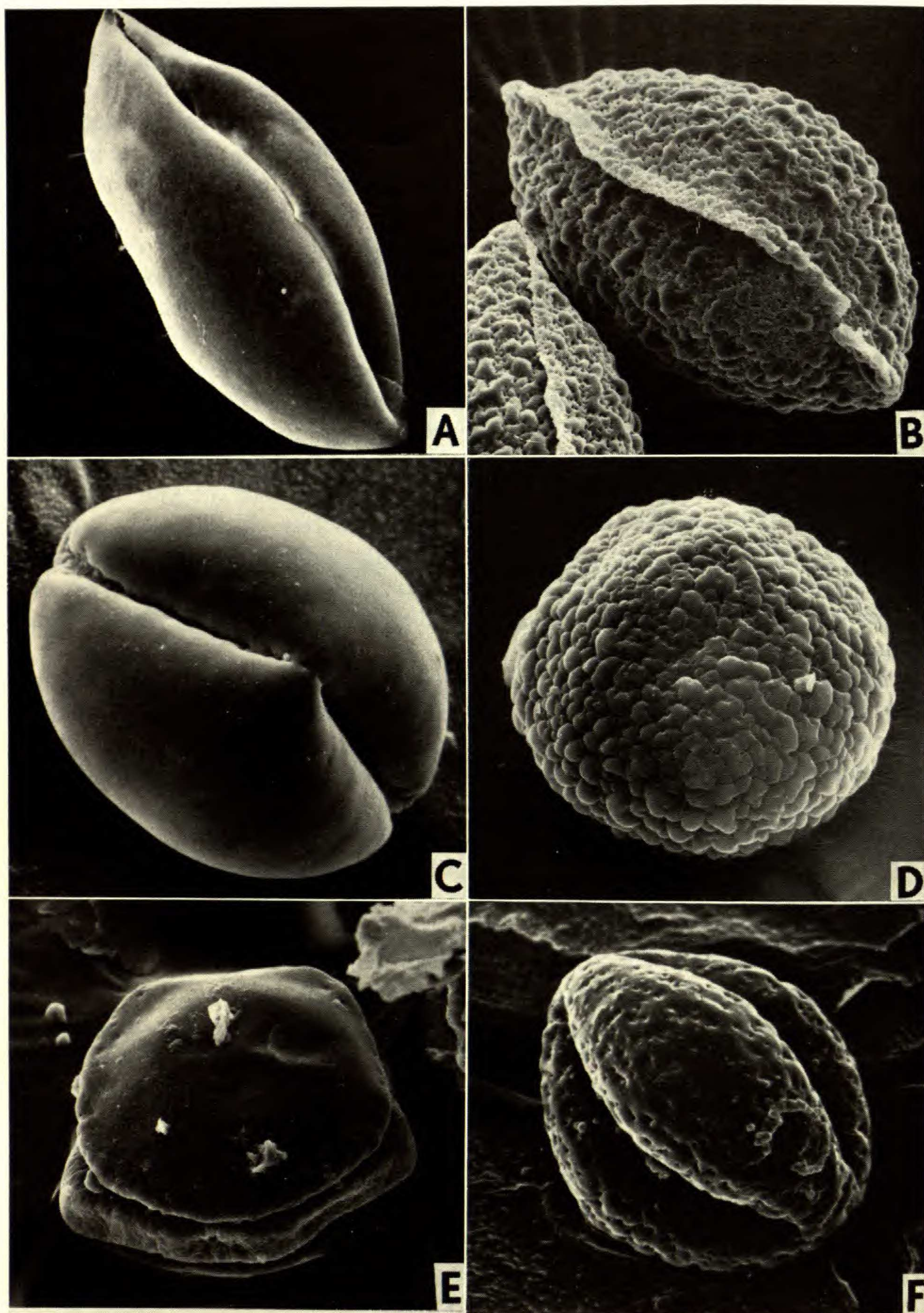


FIGURE 17. Basic types of boat-shaped and globose angiosperm pollen.—A. Boat-shaped-elongate pollen (*Anaxagorea costaricensis* R. E. Fries; Annonaceae). Presumed distal-polar view;  $\times$  ca. 1380.—B. Boat-shaped-oblong pollen (*Liriodendron tulipifera* L.; Magnoliaceae). Presumed distal-polar view;  $\times$  ca. 1440.—C. Boat-shaped-elliptic pollen (*Degeneria vitiensis* I. W. Bailey & A. C. Smith; Degeneriaceae). Distal-polar view;  $\times$  ca. 2630.—D. Globose-



TABLE 4. Classification of globose pollen based on ratio of polar to equatorial axes (P/E).

| Designation                     | P/E ratio   |
|---------------------------------|-------------|
| Prolate                         |             |
| Perprolate                      | $\geq 2.00$ |
| Euprolate                       | 1.34–1.99   |
| Subprolate <sup>a</sup>         | 1.15–1.33   |
| Prolate spheroidal <sup>a</sup> | 1.01–1.14   |
| Spherical                       | 1.00        |
| Oblate                          |             |
| Oblate spheroidal <sup>a</sup>  | 0.88–0.99   |
| Suboblate <sup>a</sup>          | 0.76–0.87   |
| Euoblate                        | 0.51–0.75   |
| Peroblate                       | $\leq 0.50$ |

<sup>a</sup> Subprolate, prolate spheroidal, oblate spheroidal, and suboblate pollen grains may be grouped together under the category of subspheroidal pollen.

with the equatorial outline of the grain, but this is not the case in equatorially constricted pollen. The amb in tricolpate (and tricolpate-derived) globose pollen especially may be of some phylogenetic significance, and there are a number of possible amb types in such pollen (cf. Fig. 18). Pollen with a round amb may be described as circular, and with respect to the relationship of apertures to the amb may be termed circulaperturate. Tricolpate or tricolpate-derived pollen without a circular amb has either concave, convex, or straight amb sides. Such pollen with straight amb sides may be described as polygonal, while pollen with concave or convex amb sides may be termed constricted-polygonal. Aperture location with respect to amb sides particularly may be an important phylogenetic character. In this regard polygonal pollen may be either angulaperturate with apertures situated in the angles of the amb sides or planaperturate with apertures situated at the mid-points of the amb sides. Constricted-polygonal pollen may be either lanceaperturate with apertures situated in the middle of the projecting parts of the concave amb sides or sinuaperturate with apertures situated in the sinuses of the concave amb sides. If constricted-polygonal pollen is deeply lobate with convex amb sides and the apertures are situated in the indentations between the lobes of the amb, the pollen may be described as fossaperturate.

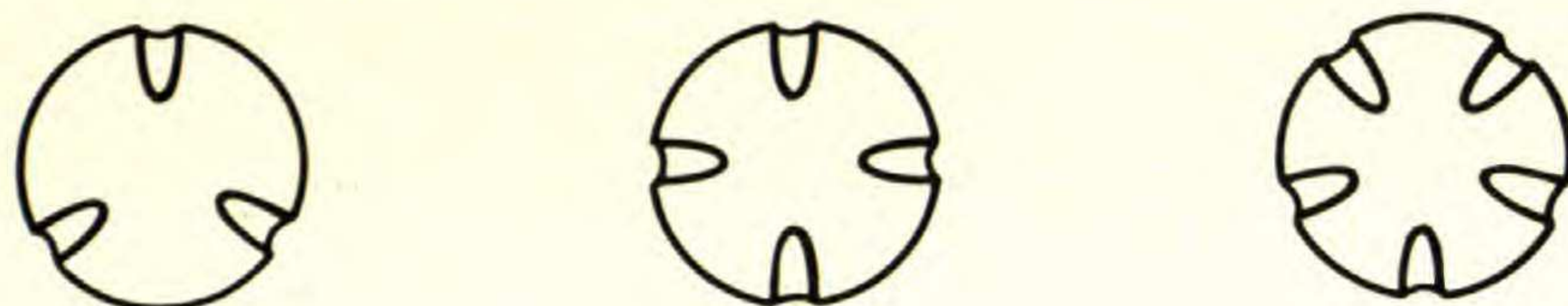
*Evolution of Pollen Grain Shape.*—As previously mentioned, pollen grain shape is largely correlated with aperture type, polarity, and symmetry. Monosulcate grains are usually boat-shaped, heteropolar, and bilateral, while colpate grains are generally globose, isopolar, and radiosymmetrical. Inaperturate pollen is normally globose, apolar, and radially symmetrical. The primitive shape of angiosperm pollen grains is clearly boat-shaped, with globose pollen representing an advanced character-state. Within boat-shaped, monosulcate pollen there appears to be an evolutionary trend from elongate (Fig. 17A) to oblong

←

spherical pollen (*Aristolochia grandiflora* Sw.; Aristolochiaceae);  $\times$  ca. 1360.—E. Globose-oblate pollen (*Eupomatia laurina* R. Br.; Eupomatiaceae). Polar view;  $\times$  ca. 1850.—F. Globose-prolate pollen (*Decaisnea fargesii* Franch; Lardizabalaceae). Equatorial view;  $\times$  ca. 1620.

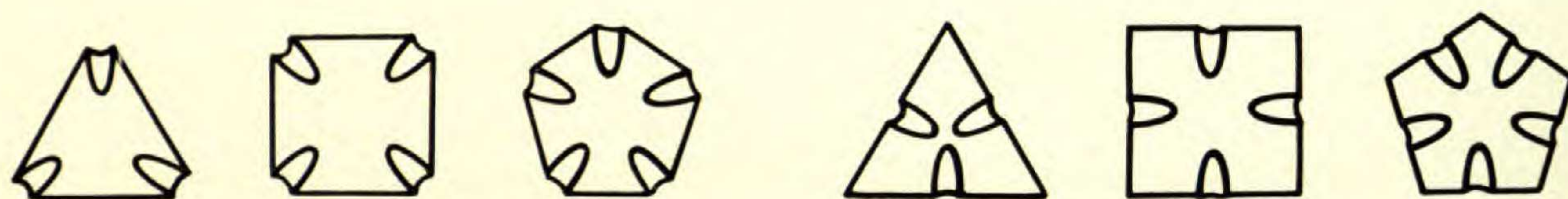


## CIRCULAR AMB



circulaperturate

## POLYGONAL AMB



angulaperturate

planaperturate

## CONSTRICTED-POLYGONAL AMB



lanceaperturate

sinuaperturate



fossaperturate

FIGURE 18. Major pollen amb types. All pollen grains shown in polar view. See text for discussion.



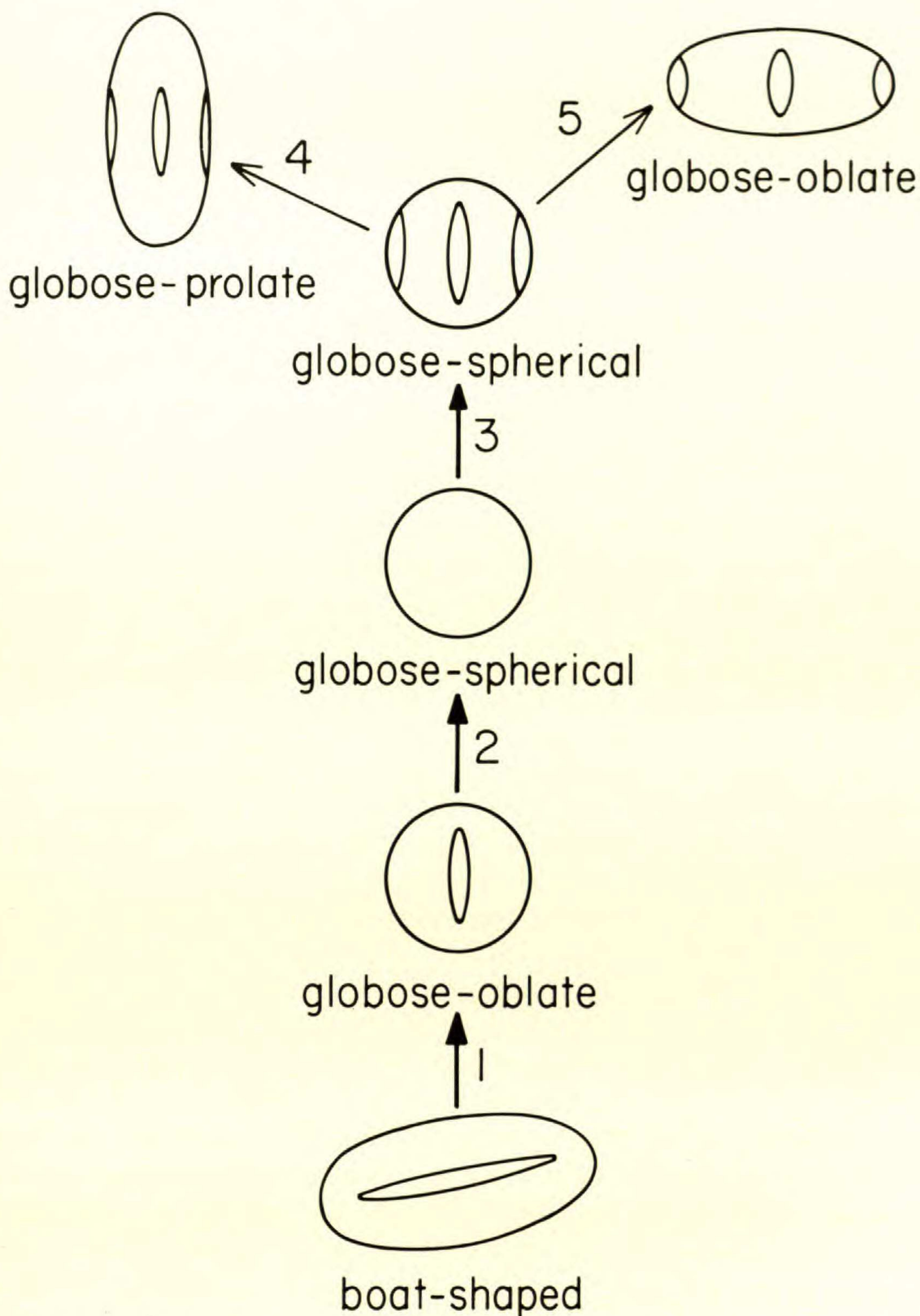


FIGURE 19. Major evolutionary trends in the shape of angiosperm pollen. Boat-shaped and globose-oblate monosulcate pollen shown in polar view; globose-spherical, globose-prolate, and globose-oblate tricolpate pollen shown in equatorial view. See text for discussion.

(Fig. 17B) to elliptic (Fig. 17C). Globose-spherical, inaperturate pollen appears to have developed from boat-shaped-elliptic pollen, generally via a more or less globose-oblate intermediate stage in which the pollen is still sulcate. Globose-spherical pollen in turn may develop into pollen which is either oblate again or prolate. The major evolutionary trends in the shape of angiosperm pollen are outlined in Fig. 19.



TABLE 5. Pollen size classes.

|                        |               |
|------------------------|---------------|
| 1) Minute grains       | $< 10\mu$     |
| 2) Small grains        | $10-24\mu$    |
| 3) Medium-sized grains | $25-49\mu$    |
| 4) Large grains        | $50-99\mu$    |
| 5) Very large grains   | $100-199\mu$  |
| 6) Gigantic grains     | $\geq 200\mu$ |

## POLLEN GRAIN SIZE

The size of pollen grains may be somewhat affected by the method of preparation and hence can be a rather unstable character. Order of magnitude, based on defined size classes, is probably the single most useful measurement of whole pollen grains. The size classes listed in Table 5 (in part after Erdtman, 1945a), based on the length of the longest grain axis (exclusive of sculpturing elements in baculate, pilate, and echinate grains) have been adopted.

Angiosperm pollen exhibits a tremendous size range, from about 2 to  $5\mu$  in *Myosotis* (Boraginaceae) to over  $300\mu$  in *Cymbopetalum* of the Annonaceae. There are approximately a dozen angiosperm families that have species of some genera with pollen grains close to or greater than  $200\mu$ , including the Annonaceae (*Annona*, *Cymbopetalum*), Nyctaginaceae (*Acleisanthes*), Malvaceae (*Kokia*), Cucurbitaceae (*Cucurbita*), Onagraceae (*Oenothera*(= *Megapterium*)), Convolvulaceae (*Ipomoea*), Polemoniaceae (*Cobaea*), Dipsacaceae (*Morina*), Xyridaceae (*Orectanthe*), Musaceae (*Musa*), Zingiberaceae, and Marantaceae. The pollen of *Cymbopetalum odoratissimum* Barb. Rodr., with some individual grains as large as  $350\mu$ , probably represents the largest fixiform pollen grain in the flowering plants (Walker, 1971a). Mention must also be made of the nonfixiform, threadlike pollen of some marine angiosperms, which may be over  $2000\mu$  long, e.g., *Zostera* (Zosteraceae) and *Cymodocea* (Zannichelliaceae).

*Evolution of Pollen Grain Size.*—Primitive angiosperm pollen (i.e., the pollen of primitive taxa in the families Magnoliaceae, Degeneriaceae, Annonaceae, Austrobaileyaceae) falls largely between  $50-99\mu$  in the large grain size class. It is therefore suggested that the primitive size of angiosperm pollen was in this size range. From large grains two different trends are apparent already within the subclass Magnoliidae—one trend toward even larger or gigantic grains (as evident within certain members of the family Annonaceae, cf. Walker, 1971b), and another trend toward smaller grains (cf. the small or minute grains in the two closely related families Saururaceae and Piperaceae). Pollen size is undoubtedly an easily reversible character and determination of the primitive size class for pollen of any particular taxon (order, family, etc.) must be based on correlation of pollen size with other characters of the taxon.

PALYNOLOGY AND THE TAKHTAJAN AND CRONQUIST SYSTEMS  
OF ANGIOSPERM CLASSIFICATION

In the following sections we will treat the 11 Takhtajan subclasses more or less in turn, considering what palynology indicates about their origins and



relationships, and noting distinctive trends within each subclass and the implications of such trends on relationships of their subgroups. Where the palynological trends are well established, in some cases on paleobotanical evidence, these comparisons will tend to confirm or negate the phylogenetic relationships and hence systematic groups proposed by Takhtajan and Cronquist; where the relationships are better established on non-palynological evidence, they may help demonstrate the direction of pollen-evolutionary trends, or indicate cases where trends break down or are reversed. Except in the Magnoliidae, Ranunculidae, and lower Hamamelididae, with which we are most familiar, we have relied heavily on Takhtajan (1966) and the classic work of Erdtman (1952) for information on the systematic distribution of pollen types; undoubtedly, a more complete and critical survey would modify some of our generalizations.

#### MAGNOLIIDAE

The Magnoliidae is putatively the most primitive subclass of dicotyledons in the Takhtajan and Cronquist systems of angiosperm classification. Palynology strongly supports this position in so much as the most primitive type of angiosperm pollen, viz., monosulcate and monosulcate-derived pollen, is restricted among dicotyledons solely to members of this subclass. Monosulcate pollen itself occurs in 15 families of the Magnoliidae (Magnoliaceae, Degeneriaceae, Himantandraceae, Annonaceae, Canellaceae, Myristicaceae, Austrobaileyaceae, Amborellaceae, Aristolochiaceae, Chloranthaceae, Lactoridaceae, Saururaceae, Piperaceae, Nymphaeaceae, and Cabombaceae), and represents the only known aperture type (exclusive of occasional trichotomosulcate variants) in eight of these families (Magnoliaceae, Degeneriaceae, Himantandraceae, Canellaceae, Austrobaileyaceae, Lactoridaceae, Saururaceae, and Cabombaceae). However, monosulcate pollen which has a particularly "gymnospermous" aspect (i.e., is strongly heteropolar, bilaterally symmetrical, and boat-shaped) is restricted largely to the families Magnoliaceae, Degeneriaceae, and Annonaceae. The polycolpate/polyporate pollen in the Chloranthaceae (*Hedyosmum* spp., *Chloranthus*) and Aristolochiaceae (*Asarum* spp.) is unique among colpate pollen in being monosulcate-derived, while tricolpate or tricolpate-derived pollen itself occurs in the families Illiciaceae, Schisandraceae, and Nelumbonaceae.

Within the Magnoliidae, atectate pollen (i.e., primitively columellaless pollen) occurs in the families Magnoliaceae, Degeneriaceae, Eupomatiaceae, and Annonaceae, and may be present also in the Himantandraceae and some Nymphaeaceae. Most magnoliid pollen, however, is tectate (cf. Walker, 1974b). Taxa within the subclass that have semitectate pollen include a few Annonaceae (e.g., *Deeringothamnus*), some Myristicaceae (e.g., *Myristica*, *Osteophloem*, *Horsfieldia* spp.), all Winteraceae, Illiciaceae, and Schisandraceae, *Saruma* of the Aristolochiaceae, and some Chloranthaceae (*Chloranthus* spp., *Sarcandra*). Intectate pollen is very rare, occurring as far as is known in only two genera of the Annonaceae (*Ophrypetalum*, *Trigynaea*) and in some species of the myristicaceous genus *Horsfieldia*.

Takhtajan's order Magnoliales (with one exception) appears to represent a



close-knit group palynologically. Its members are held together by a number of pollen characters, although in some instances these common pollen characters may occur only in the primitive taxa within a particular family. Unifying palynological characteristics of this order are seen in pollen which is frequently monosulcate, atectate to tectate-imperforate, more or less psilate, large to medium-sized, solitary, heteropolar, bilateral to isobilateral, and boat-shaped to globose-oblate. The greatest pollen diversity in the subclass occurs in the magnolialean family Annonaceae, where pollen characters have proved especially useful for infrafamilial classification (cf. Walker, 1971b, 1972a). The similar medium-sized, more or less psilate, tectate-imperforate, globose-oblate, isobilateral monosulcate pollen which occurs in certain members of the families Canellaceae and Myristicaceae (e.g., *Warburgia* and *Dialyanthera*) seems indicative of a close relationship between these two families. Although pollen of the Eupomatiaceae is atectate, psilate, medium-sized, and solitary, it departs somewhat from that of other members of the order in being zonosulcate. The family Winteraceae, however, is completely disharmonious within the order in having anaulcerate, semitectate-reticulate, radiosymmetric, globose-spherical pollen which is in permanent tetrahedral tetrads. In terms of its semitectate-reticulate exine structure, winteraceous pollen more closely resembles pollen of the Illiciaceae-Schisandraceae. Palynological data strongly oppose Hutchinson's (1964) placement of *Degeneria* (with its anasulcate, atectate, bilateral, boat-shaped, solitary pollen) within the Winteraceae.

The order Laurales, sensu Takhtajan, by contrast is characterized largely by inaperturate, more or less sculptured, apolar, radiosymmetric, globose-spherical pollen grains (e.g., most Monimiaceae, and all Hernandiaceae, Gomortegaceae, Lauraceae, and Gyrocarpaceae). Interestingly, the otherwise primitive Austrobaileyaceae possess well-developed monosulcate pollen, and pollen grains of the primitively vesselless Amborellaceae may be either inaperturate or sulcoidate. Pollen of the Calycanthaceae, Atherospermataceae, and the newly described Idiospermaceae (cf. Blake, 1972) is disulcate. The echinate pollen of *Peumus* in the Monimiaceae shows a resemblance to the echinate pollen of the Hernandiaceae in that spines which occur on the pollen in both of these families are made up of separate, cable-like subunits. On the other hand, a different type of echinate pollen characterizes the families Gomortegaceae, Lauraceae, and Gyrocarpaceae, which appear to represent a close-knit group. The families Chloranthaceae and Lactoridaceae show little or no relationship palynologically to the rest of the order. Although pollen of *Lactoris* is in permanent tetrads, it appears to have little else in common with pollen of the Winteraceae. Pollen morphology supports the naturalness of the Piperales, sensu Takhtajan, since both the Saururaceae and Piperaceae have distinct, small to minute, monosulcate pollen which does not occur elsewhere in the subclass. Pollen morphology of the Aristolochiaceae supports its isolated position in a monotypic order. The great diversity of pollen types which characterizes the genera of Nymphaeales supports the idea that this is a very old order and also supports the separation of Nymphaeaceae, sensu lato, into a number of separate families. For example, most members of the Nymphaeaceae, sensu stricto, possess a distinctive aperture (a zonosulculus) found elsewhere in the subclass only in the Eupomatiaceae.



The pollen morphology of some magnoliid families is indicative of relationships with other dicotyledonous subclasses. For example, there is a strong similarity in pollen size, sculpturing, exine stratification, and apertures between pollen of the Chloranthaceae and certain "lower" Hamamelididae (e.g., Cercidiphyllaceae, Trochodendraceae, Tetracentraceae, Eupteleaceae). Some ranunculid pollen (e.g., that of the menispermaceous genus *Tinospora*) exhibits great similarity to the pollen of the Illiciaceae-Schisandraceae, which appear to represent a connecting link between magnoliid and ranunculid dicots, cf. placement of these two families by Cronquist (1968) and Takhtajan (1969). Pollen grains of both *Tinospora* and *Schisandra* show similarity in being semitectate-reticulate and polarly syncolpate, and pollen of these two genera possesses the same peculiar linear median thickening in the colpi. For further details on the pollen of the subclass Magnoliidae, see Walker (1974b, 1974c, 1975, 1976).

#### MONOCOTYLEDONAE

Like the Magnoliidae, the monocotyledons are a basically monosulcate group, and they illustrate many of the same trends and problems we have already considered. Although certain monosulcate-derived aperture conditions are more prevalent among monocots than in magnoliid dicots, there are some members of both groups which retain the essentially gymnospermous boat-shaped monosulcate type which is believed on both comparative and fossil evidence to be basic to angiosperms as a whole. Hence we must look at features other than aperture condition for any of the distinctive specializations which we might expect if the monocots represent a major monophyletic group within the angiosperms. One such specialization may be a tendency for open-reticulate or semitectate exine structure on most of the grain surface with finer tectate or tectate-perforate structure at the "bow" and "stern" and near the sulcus margins. Such pollen is found among some of the oldest angiospermous monosulcates of the Lower Cretaceous—being described under the form-genera *Retimonocolpites* and *Liliacidites* (Doyle, 1973; Wolfe et al., this symposium)—and is found also in representatives of all four monocot subclasses, including some of their putatively more primitive members (e.g., Butomaceae, Liliales, Bromeliaceae, Araceae, Palmae), but not in magnoliid dicots. This distribution is consistent with the hypothesis (suggested by Doyle, 1973) that the *Liliacidites*-type is basic for the monocotyledons, although the fact that other monocots have more uniformly tectate exines means that further comparative studies are needed.

*Alismatidae*.—In the generally aquatic monocot subclass Alismatidae, monosulcate pollen of the *Liliacidites*-type is found in the genus *Butomus*, which is often considered the most primitive member of the subclass. Most other Alismatidae are more specialized in their pollen morphology, in keeping with the other specializations which rule them out as the direct ancestral complex for the monocots (e.g., seeds without endosperm, trinucleate pollen: cf. Cronquist, 1968; Takhtajan, 1969). All members of the Alismatales except *Butomus* are polyforate, with 4–20 scattered pore-like apertures. The Hydrocharitales and Najadales show loosely correlated tendencies for loss of the sulcus (still seen in some Hydrocharitaceae and Aponogetonaceae) and reduction in sculpture, so that most of them are



inaperturate, often with thin, finely spinulose exines, analogous to those noted in the Laurales. The culmination of this trend is apparently seen in the marine members of these orders: here the pollen consists of flexible, "non-fixiform" threads up to 2 mm long, whose walls consist entirely of cellulosic intine. Since this specialization occurs in marine members of both Hydrocharitales (Thalassioideae and Halophiloideae) and Najadales (Zosteraceae, Posidoniaceae, Cymodoceaceae), it presumably represents an independent, convergent adaptation to marine conditions.

*Liliidae*.—The subclass Liliidae includes a much larger proportion of members with the primitive monosulcate condition, many with the *Liliacidites*-type of sculpture differentiation (e.g., Liliaceae, Amaryllidaceae, Stemonaceae). Other monosulcate-derived aperture types seen in the Liliales and Iridales are trichotomosulcate, operculate-monosulcate, disulculate, and diulculate. Although the coexistence (e.g., in Agavaceae) of operculate and zonosulcate types suggests a mode of origin for zonosulcates similar to that postulated in the Nymphaeaceae (see above), the elongate shape of the diulculates (e.g., *Colchicum*), with the ulculi located at the ends of the grain, suggests that the two apertures may represent cut-off ends of the sulcus. Other Liliales show a reduction trend leading to inaperturate, often finely spinulose grains (e.g., Smilacaceae), while a few show the unusual spiraperturate condition (Aphyllanthaceae, some Xanthorrhoeaceae), seen also in the commelinid family Eriocaulaceae.

The Zingiberales, which Cronquist places in the Commelinidae and Takhtajan in the Liliidae, illustrate an extreme case of the reduction trend: in most of them, the exine is reduced to small, acetolysis-resistant spinules, and the intine is thickened proportionately (cf. Skvarla & Rowley, 1970). There are only rare vestiges of the single distal aperture (Heliconiaceae, *Zingiber*; Kuprianova, 1948); hence we would suggest that the polyforate to spiraperturate condition seen in Costaceae represents secondary origin of apertures. Finally, the Orchidaceae show a striking trend, analogous to that seen in the Apocynaceae and Asclepiadaceae among the dicots, from single grains (sometimes reticulate and monosulcate) to tetrads, polyads, massulae, and highly specialized pollinia consisting of the entire contents of an anther locule.

*Commelinidae*.—The most striking trend in the subclass Commelinidae, apparently tied to the shift there to wind pollination, leads from monosulcate to the monoulcerate (monoporate) condition seen in grasses. Although Cronquist (1968) groups the grasses and sedges in the order Cyperales, palynology favors Takhtajan's (1969) interpretation of the two groups as more distantly related, the grasses being derived from the Restionales and the sedges from the Juncales. Monosulcate pollen occurs in the Bromeliales and Commelinales, but in the Restionales we find a transitional series from irregular-aperturate (Centrolepidaceae, some Restionaceae) to essentially graminoid monoulcerate grains (Flagellariaceae, other Restionaceae; cf. Chanda, 1966). Most sedges, on the other hand, have very peculiar asymmetrical, ovoid grains with one or four blotchy apertures, which are referred to as pseudomonads or cryptotetrads, since each grain is derived from one pollen mother cell by degeneration of three of the haploid nuclei (cf. Cranwell, 1953; Dunbar, 1973). This is readily imagined as a specialization



from the situation in the Juncaceae, which have ulceroidate grains united in permanent tetrads.

*Arecidae*.—The last monocot subclass, the Arecidae, shows most of the aperture and exine structure trends exhibited by the other monosulcate groups, as well as some of its own. Sowunmi (1968, 1972) and Thanikaimoni (1970b) have inferred a variety of aperture trends in the palms, from the widespread, often reticulate monosulcate condition to trichotomosulcate, ulcerate, and, by extension of the furrow all around the grain, to the zonosulcate condition in the unique, spiny grains of *Nypa*. The two furrows of the Lepidocaryoideae are postulated to have arisen either by constriction of the middle of an extended distal sulcus (Thanikaimoni, 1970b), or of the two polar portions of a complete zonosulcus of the *Nypa* type (Sowunmi, 1968); in either case, the furrows must be longitudinal and hence analogous to the colpi of higher (dicolpate) dicotyledons rather than the sulculi of many Magnoliidae. Diporate grains may have arisen either by contraction of such colpi (Thanikaimoni) or isolation of the ends of a sulcus (Sowunmi).

The Araceae show both *Liliacidites*-type monosulcates and still more of the basic monosulcate-derived types, including "ephedroid" striate monosulcates, spinulose inaperturates, and polyforates (cf. Thanikaimoni, 1969). Spinulose grains with a reduced aperture occur in the Lemnaceae, consistent with their postulated derivation from the Araceae. Finally, the characteristic ulcerate, usually reticulate grains of Pandanaceae, Sparganiaceae, and Typhaceae, similar to those in some Cyclanthaceae, support Takhtajan's (1969) grouping of these three families in the Arecidae.

#### NON-MAGNOLIID DICOTYLEDONAE

With the problematical exception of *Nelumbo* (which Takhtajan in fact refers to the Ranunculidae), all the groups considered so far have had monosulcate and monosulcate-derived pollen types. In contrast, the remaining six subclasses of non-magnoliid dicots have exclusively tricolpate and tricolpate-derived pollen types. Unfortunately, neither modern nor fossil evidence indicate clearly how tricolpate pollen originated. The two most commonly postulated intermediates between the monosulcate and tricolpate conditions are trichotomosulcate (giving rise to tricolpate by isolation of the three arms of the furrow: Straka, 1963; Wilson, 1964) and inaperturate (with colpi arising *de novo*: Muller, 1970; Walker, 1974c). Difficulties with the trichotomosulcate hypothesis include the rarity of trichotomosulcates among possibly related magnoliid dicot groups, and the difference in orientation (with reference to the other grains in the meiotic tetrad) of the three arms in trichotomosulcate grains (according to "Garside's law," meeting in four groups of three) and the three colpi of tricolpates (according to "Fischer's law," meeting in six groups of two) (cf. Erdtman, 1969). However, the extinct hypothetical ancestors of the tricolpates need not have had the same orientation as in those modern trichotomosulcates where it is known (mostly monocots). A strong case has been made for the *de novo* origin of several equatorial apertures from inaperturate ancestors in the Chloranthaceae and Aristolochiaceae; again, it is uncertain whether analogies can be drawn to the situation in non-magnoliid dicots, with their regularly three-fold symmetry. Furthermore, it is not clear whether the



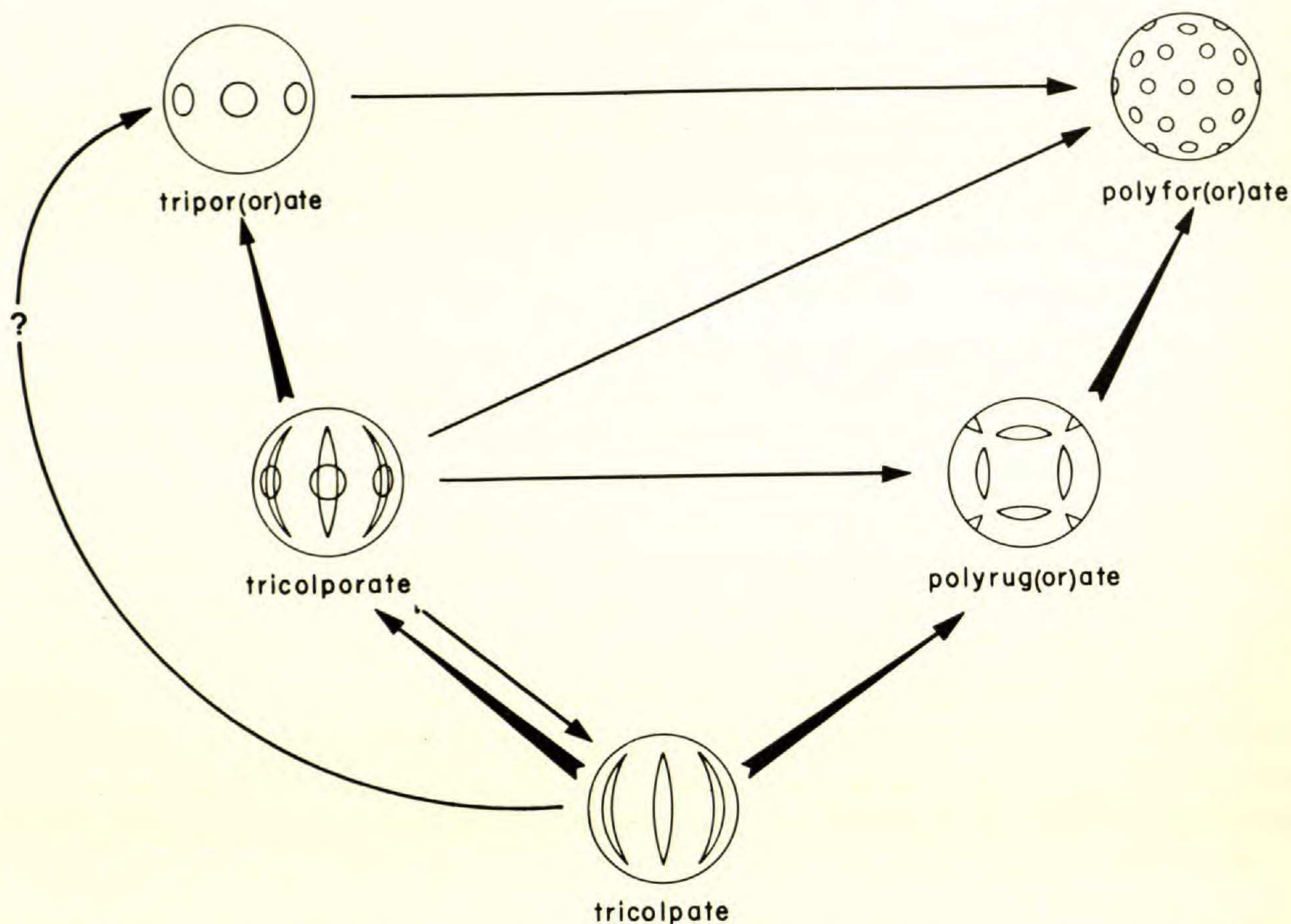


FIGURE 20. Principal evolutionary transformations in pollen aperture condition in non-magnoliid dicotyledons. Thick arrows indicate major trends, fine arrows less important ones. Parentheses indicate cases where ora may or may not be present, depending on the group in question. See text for discussion.

tricolpate condition arose once or several times, and hence whether the six non-magnoliid subclasses form a monophyletic group within the dicots, or simply a grade or level of advancement (cf. Wolfe et al., this symposium). Studies of both modern and fossil tricolpates and their possible non-tricolpate relatives are desirable to test hypotheses on the origin of tricolpates, and especially to identify the one or more monosulcate ancestors or "sister groups" of the tricolpate subclasses.

Among the trends affecting tricolpate groups (Fig. 20), probably the most important is the origin of compound apertures, resulting in the tricolporate condition, with round or variously elongate thin areas (ora) at the centers of the colpi. Tricolporoidates, where the ora are poorly defined (oroids), represent an intermediate condition. Tricolporate grains are in fact numerically dominant in the modern dicot flora. This trend is directly documented from the Cretaceous fossil record (Doyle, 1969; Muller, 1970; Wolfe et al., this symposium), quite independently of the comparative morphological evidence on which it was originally postulated (e.g., by Takhtajan, 1959). In a few groups, there is evidence for apparent reversal of the main tricolpate-tricolporate trend by reduction of the ora, resulting in secondarily simple apertures. A well-documented trend runs from tricolpate to polyrugate, with many furrows or rugae scattered globally over the surface of the grain, and by shortening of the rugae to polyforate,



with numerous scattered pore-like apertures or foramina. Polyrug(or)ate and polyfor(or)ate grains may also be derived from compound-aperturate ancestors.

The triporate and triporate conditions, with respectively simple and compound round equatorial apertures, represent still additional specializations from the tricolpate condition. It is quite uncertain whether triporate grains have ever arisen directly from tricolpate ancestors by shortening of simple colpi. A few morphological series indicate that simple triporates may arise from tricolporates by a gradual in-place-disappearance of the colpi (i.e., via tricolpoidorate intermediates). In most cases, however, there is evidence that triporates arose from tricolporates by shortening of the furrows (i.e., via brevitricolporate intermediates); here the resulting forms are often clearly pororate. Subsequent reduction could lead to apparently simple pores, as in the minute grains of many Urticales.

*Ranunculidae*.—Within the first tricolpate-derived subclass, the Ranunculidae, many Ranunculales (some Ranunculaceae, Lardizabalaceae, Menispermaceae, Berberidaceae sensu lato) retain simple, often finely reticulate tricolpate pollen of the type first seen in the Lower Cretaceous fossil record (cf. Doyle, 1969; Muller, 1970; Wolfe et al., this symposium). Although a few Menispermaceae (and Lardizabalaceae?) are tricolporate, most Ranunculidae have simple apertures; in fact, the compound (tricolporate) apertures of *Paeonia* are one of the reasons for believing that this genus belongs neither in the Ranunculaceae nor the Ranunculidae, but rather in the Dilleniidae. Especially in the Ranunculaceae, there is a series leading from tricolpate through polyrugate to polyforate grains, with a precisely defined geometric relationship of the apertures ("successiformie" of Van Campo, 1967), and often with granulate aperture membranes and small supracteal spinules. Occurrence of the same trends in the Papaverales and the Caryophyllidae (see below) supports the hypothesis that these two groups are derived from Ranunculales (Van Campo, 1967; Roland, 1971).

Problematical aperture situations are seen in the Illiciaceae and Schisandraceae, considered to constitute the most primitive order (Illiciales) of the Ranunculidae by Takhtajan (1969), but retained in the Magnoliales by Cronquist (1968). *Illicium* is reticulate and tricolpate, but the three colpi meet at the poles (syncolpate). *Kadsura* and most *Schisandra* species are hexacolpate, with three short colpi alternating with three which join at one pole, but *Schisandra grandiflora* has just three colpi which join at one pole, presumably corresponding to the three fused colpi of the other species. All three types may represent specializations from a simple tricolpate condition, but an intriguing possibility is that the *S. grandiflora* type represents a unique survivor of the three-armed intermediate postulated by the trichotomosulcate theory.

*Hamamelididae*.—Reticulate tricolpate pollen, often with granulate colpus membranes, is also retained by some of the putatively more primitive members of the subclass Hamamelididae, such as *Trochodendron*, *Tetracentron*, *Cercidiphyllum* (with somewhat anomalous ill-defined apertures), *Platanus*, and most Hamamelidaceae. A few Hamamelididae, such as *Euptelea*, some Hamamelidaceae (*Chunia*, *Sycopsis*), and occasionally *Platanus*, vary from tricolpate to hexarugate. In marked contrast, most of the "higher" Hamamelididae or classic



"Amentiferae," i.e., Betulaceae, Myricaceae, *Casuarina*, *Rhoiptelea*, Juglandaceae, Ulmaceae, Moraceae, Cannabaceae, and Urticaceae, have much more advanced triporate or derived (diporate, polyporate) pollen types. Although some Hamamelidaceae (*Liquidambar*, *Altingia*) have pores, these are simple, presumably rugate-derived foramina, whereas most porate Amentiferae have clearly compound apertures (i.e., they are actually pororate). This suggests that the triporate Amentiferae were not derived directly from simple-aperturate forms (as in all Hamamelidales except *Rhodoleia*), but rather from tricolporate ancestors by shortening of the colpi. In some Amentiferae, such as *Rhoiptelea*, a presumed primitive relative of the Juglandaceae, and *Planera* (Ulmaceae), somewhat misleadingly described by Erdtman (1952) as colpate, the outer apertures are in fact short colpi. Furthermore, Upper Cretaceous fossil sequences show apparently transitional series from triangular tricolporates of a type more characteristic of Rosidae than Hamamelidales (see below), through triangular triporates of the so-called Normapolles complex (many of which have features, such as *arci*, suggestive of *Rhoiptelea*, Betulaceae, Ulmaceae, etc.), to essentially amentiferous types (Góczán et al., 1967; Doyle, 1969; Muller, 1970; Wolfe et al., this symposium). Tricolporate grains do occur in some Hamamelididae, such as *Rhodoleia*, Fagaceae, *Eucommia* (with a peculiar asymmetry in the length of the colpi), *Barbeya*, and *Leitneria*, but except perhaps for *Trigonobalanus* in the Fagaceae (Erdtman, 1967), they show few tendencies toward the triangular tricolporate intermediate condition inferred from the fossil record. Finally, the higher Hamamelididae investigated differ from the Hamamelidales in having granulate rather than columellate infratectal exine structure, but such structure is found in some Rosidae (Van Campo & Lugardon, 1973).

*Caryophyllidae*.—Whereas palynology thus casts some doubt on the naturalness of the Hamamelididae, it strongly confirms the unity of the subclass Caryophyllidae, especially the core orders Caryophyllales and Polygonales, and their postulated derivation from the Ranunculidae. Within several families (Phytolaccaceae, Nyctaginaceae, Cactaceae, Portulacaceae, and Caryophyllaceae) we see both the same type of tricolpate pollen with granulate colpus membranes and supracteal spinules as in the Ranunculaceae, and the same trend from tricolpate through polyrugate to polyforate (cf. Van Campo, 1967; Roland, 1971). In keeping with their high degree of specialization and postulated close relationship, the Chenopodiaceae and Amaranthaceae are exclusively polyforate. Finally, the Polygonaceae show sculpture and aperture trends comparable to those in the Caryophyllales, but they are more specialized in having compound apertures. It may be noted that there is no palynological indication of the heterogeneity of the Caryophyllidae inferred from chemical data (cf. Fairbrothers et al., this symposium).

*Comparison of Dilleniidae and Rosidae*.—Most of the orders in the next two subclasses, Dilleniidae and Rosidae, appear to be basically tricolporate rather than tricolpate, and hence in this character more specialized than the preceding subclasses (except "higher" Hamamelididae or "Amentiferae"). A few members have tricolpate pollen, but in most cases their relatively advanced position as inferred from other characters and comparisons with related groups suggest that



this is a result of secondary reduction of ora from tricolporate ancestors, resulting in an apparent reversal of the tricolpate-tricolporate trend (see below). The most convincing examples of retention of the primitive tricolpate condition are seen in some Dilleniaceae, where *Hibbertia* and several other genera have reticulate tricolpate pollen associated with putatively primitive non-palynological features, while others (*Davilla*, *Tetracera*, etc.) are tricolporate (Dickison, 1967).

Although there are some distinctive trends which tend to unify and relate various orders within the Dilleniidae and Rosidae, the more primitive pollen types and many of the most basic trends are so similar that palynological evidence is ambiguous on whether the two subclasses as a whole represent two such distinct major groups as indicated by the Takhtajan and Cronquist systems. One of the most important of these parallel trends concerns size and the degree of differentiation of exine and aperture structure. Some members have small, thin-walled, psilate or finely reticulate tricolporoidate pollen, whereas others have larger, thicker-walled, and sometimes highly sculptured pollen with well-developed ora, thickened colpus margins, and other endexinal specializations. That this reflects an *elaboration* trend was originally inferred from comparative studies of modern tricolporate groups (Van Campo, 1946, 1966; Dahl, 1952; Muller, 1969a), and is confirmed by observation of a stratigraphic elaboration trend among the first tricolporates of the early Upper Cretaceous (cf. Muller, 1970; Doyle, 1973; Wolfe et al., this symposium). Curiously, this appears to represent reversal of a still earlier size and sculpture reduction trend seen among their presumed late Lower Cretaceous tricolpate ancestors (Doyle, 1969). In any case, caution must be used in generalizing these trends to modern groups: while the fossil evidence may indicate that all large tricolporates are more advanced than at least some small tricolporoidates, small size cannot be interpreted so simply, since secondary decrease in size is both easy to imagine and strongly inferred in some cases (e.g., *Myosotis*).

*Dilleniidae*.—Within the Dilleniidae, most of the more generalized tricolporate forms would be difficult to exclude from the Rosidae; they differ from the latter more on the absence of the “rosid” shape and aperture trends discussed below. An area in which to seek more positive dilleniid specializations may be comparative developmental studies of exine structure, e.g., to determine whether other types in the subclass can be interpreted as variations on the “tilioid” type, with a reticulum formed of an undulate tectum, cited by Van Campo & Lugardon (1973) as seen in the “Dilleniales” (Dipterocarpaceae) and Malvales (Van Campo, personal communication).

Groups of Dilleniidae with small, relatively unsculptured tricolpor(oid)ate grains include many Ochnaceae (Muller, 1969a), the subfamily Ternstroemiaceae of the Theaceae (Keng, 1962), Marcgraviaceae, Hypericaceae, and Elatinaceae within the Theales; Lacistemataceae, many Flacourtiaceae (usually finely reticulate rather than psilate), Datisceae, and Begoniaceae in the Violales (sensu lato); Cyrillaceae and Saurauaceae in the Ericales; and Elaeocarpaceae in the Malvales. Groups with more advanced, larger, thicker-walled tricolporate pollen include *Ochna* and a few other Ochnaceae, the subfamily Camellioideae in the Theaceae, Dipterocarpaceae, Quinaceae, and Guttiferae (often with very



thick exines) in the Theales; Violaceae, Bixaceae, Cistaceae, and those families considered advanced members of the Violales by Cronquist but segregated as the Passiflorales by Takhtajan; and many Tiliaceae and some Sterculiaceae in the Malvales. These characters agree roughly with the relative advancement of these families in the Takhtajan and Cronquist systems.

The reticulate, prolate tricolporoidate pollen of *Salix* (placed in the Amentiferae in the Englerian system) is more consistent with Takhtajan and Cronquist's derivation of the Salicaceae (including also the inaperturate *Populus*) from the Violales, specifically the Flacourtiaceae. However, since both some *Salix* species and the putatively related Frankeniaceae and Tamaricaceae are described as tricolpate, this derivation requires reversal of the major tricolpate-tricolporate trend. Similarly, in the Capparales the Cruciferae are described as tricolpate (occasionally hexacolpate, etc.), whereas the putatively more primitive Cappara-ceae, Tovariaceae, and Moringaceae have generally tricolporate pollen. Other candidates for reversion are seen in the Primulales, where the Myrsinaceae and Theophrastaceae are usually tricolporate, while the Primulaceae include tricolpates as well as syncolpates and pollen with increased numbers of apertures.

Several dilleniid orders exemplify peculiar pollen types and trends, some of which have no close analogs in the Rosidae. Within the Ericales, the Saurauiaceae, Actinidiaceae, Clethraceae, and Cyrillaceae have simple, relatively smooth tricolporate grains (consistent with their postulated transitional relationship to the Theales), but most Ericaceae, Pyrolaceae, and Empetraceae have permanent tetrads, while the Epacridaceae have tetrads consisting of one viable and three abortive grains, representing an unusual mode of reversion to functional monads. The Malvales are very diverse palynologically, but the existence of intermediate conditions and "reticulate" similarities between families supports the concept that they form a natural group. In agreement with their postulated primitive position, the Elaeocarpaceae have small, smooth, tricolporoidate pollen. Among the more specialized conditions in the order are oblate triporate or brevicolporate grains in Bombacaceae and some Tiliaceae (e.g., *Tilia*) and Sterculiaceae (with the apertures on the flat or concave sides of the grains, rather than at the angles as in many Rosidae), and large polyforate grains with prominent spines in Malvaceae and some Sterculiaceae. The fact that the Sterculiaceae include both generalized tricolporates and most of the advanced types found in the other families suggests they may be a paraphyletic (grade) taxon consisting of primitive relatives (sister-groups) of the higher groups. The Ebenales also show a diversity of relatively advanced pollen types: fairly large tricolporates in Styracaceae and Ebenaceae, thick-walled tetracolporates in Sapotaceae, and oblate-triangular brevitricolporate to triporate grains (more suggestive of Rosidae) in Symplocaceae. Here the connections are less evident than in the Malvales, and further palynological study might be of interest in evaluating the naturalness of the group and its postulated derivation from the Theales.

*Rosidae*.—The same size and sculpture elaboration trend as seen in the Dilleniidae can be seen in the Rosidae. Small, finely reticulate or psilate tricolporoidate pollen is especially common in the Saxifragales (Cunoniaceae, Davidsoniaceae, Escalloniaceae, Hydrangeaceae, Crassulaceae, and Saxifraga-



ceae sensu stricto), in keeping with the postulated basal position of this order, and in some Araliaceae, Cornaceae (e.g., *Curtisia*), and Celastrales (e.g., Phelliniaceae, some Celastraceae). Larger tricolporate pollen, often with elaborate colpus margins and ora, is typical of most Pittosporaceae, Rosaceae, legumes (except Mimosaceae: see below), Rutales, Sapindales, Cornales (e.g., *Nyssa*, *Cornus*, *Mastixia*), Rhamnaceae, Vitaceae, Celastrales, and Oleaceae.

Even within the most primitive of these groups (e.g., Cunoniaceae, Saxifragaceae), certain tendencies are seen which are widespread throughout the Rosidae but very rare in the Dilleniidae, especially oblate-triangular grains with apertures at the angles (breviaxy, discussed by Van Campo, 1966), syncolpy, reduction to the dicolp(or)ate condition, and striate sculpture. Groups with oblate-triangular, angulaperturate grains, occasionally syncolpate, include many Cunoniaceae, Araliaceae, Myrtaceae (see below), Burseraceae, Simaroubaceae, Sapindaceae, Humiriaceae, Vochysiaceae, Nyssaceae, Icacinaceae and other Celastrales, Rhamnaceae, Vitaceae, and Elaeagnaceae. The prevalence of this trend to triangular shape and shortening of apertures in the Rosidae has been mentioned above as evidence that the triporate "Amentiferae" or higher Hamamelididae are more closely related to the Rosidae than to the Hamamelidales (cf. also Wolfe et al., this symposium). Dicolporate grains, often extremely small, are seen in Cunoniaceae, Eucryphiaceae, Myrtaceae, Crypteroniaceae (placed in Saxifragales by Takhtajan, Myrtales by Cronquist), and Corynocarpaceae (Celastrales according to Takhtajan; palynology hence contradicts Cronquist's placement of this family in the Ranunculales). Striate grains are common in Saxifragaceae, Crassulaceae, Rosaceae, Caesalpiniaceae, Anacardiaceae, Burseraceae, Simaroubaceae, Rutaceae, Cneoraceae, Aceraceae, Hippocastanaceae, Melianthaceae, Vochysiaceae, Krameriaceae, Loranthaceae, etc.

The Myrtales and Santalales show what may be interpreted as special elaboration of these "rosid" trends. Interestingly, the Lythraceae and Olacaceae, considered the most primitive members of their respective orders by Takhtajan and Cronquist, bear much the same palynological relationship to the other members as do the Sterculiaceae to the other Malvales.

The Myrtales include not only a few members with prolate tricolporate pollen (Punicaceae, some Lythraceae, Rhizophoraceae), but also a variety of other types: triangular tricolporates, often syncolpate, in Myrtaceae and Lythraceae (associated with striate sculpture in *Cuphea*); prolate triporates (resulting from disappearance in place rather than shortening of colpi?) in Sonneratiaceae and some Lythraceae (the origin of the large, sculptured grains of *Sonneratia* from smaller, more lythraceous precursors is documented by the fossil record: Muller, 1969b); large, thick-walled triangular triporates in Onagraceae; and forms with three colporate apertures alternating with three (*de novo*?) pseudocolpi in Combretaceae, Melastomataceae, Penaeaceae, and some Lythraceae and Oliniaceae. It may be noted that these "rosid" palynological trends contrast with "dilleniid" features in the leaf architecture of the Myrtales (Hickey & Wolfe, this symposium); further study is desirable to determine which set of similarities are the result of convergence.

In the Santalales, the vegetative trend to parasitism is rivalled by equally



bizarre trends in pollen morphology. Relatively unspecialized triangular tricolporates exist in some Olacaceae, Opiliaceae, and Octoknemaceae; syncolpates (often heteropolar) in other Olacaceae, Santalaceae, and Loranthaceae. The *Anacolosa*-type (Olacaceae), with three pores located on each hemisphere of an oblate triangular grain, may be related to the latter type. Finally, a few Olacaceae have strikingly "proteaceous" triangular triporate grains, possibly providing a clue to the relationships of the otherwise enigmatic Proteaceae, although similar types are also seen in the Icacinaceae (Celastrales) (cf. Erdtman, 1952; Muller, 1970).

Several other unusual or problematical trends seen in the Rosidae may be mentioned. Multiplication of the number of equatorial colporate apertures has occurred in several groups, with the Bruniaceae and Polygalaceae (up to 28-colporate) representing the most extreme cases. Candidates for reversal of the tricolpate-tricolporate trend are seen in the Linales and Geraniales: the woody members (many Humiriaceae, Erythroxylaceae, Zygophyllaceae, etc.) tend to have tricolporate pollen, while some members of the more typically herbaceous families (Linaceae, Oxalidaceae, Geraniaceae) are described as tricolpate. Finally, among the legumes the Mimosaceae show a great array of tetrad and polyad types and peculiar, asymmetric porate grains apparently representing secondary monads. Other Mimosaceae (e.g., *Leucaena*, *Neptunia*, *Prosopis*) have more "normal" tricolporate monads suggesting links with the related Caesalpiniaceae and Papilionaceae; however, Guinet (1966, 1969) has shown that within *Leucaena* and other genera these tricolporate grains can be connected through asymmetric tricolporate forms to obvious secondary monads, suggesting that the compound condition may actually be primitive in the family.

The two most important cases in which the Takhtajan and Cronquist systems differ on whether a group should be placed in the Dilleniidae or Rosidae involve the Lecythidaceae (Rosidae, in fact Myrtales according to Takhtajan, Dilleniidae according to Cronquist) and the Euphorbiales (Dilleniidae near Malvales according to Takhtajan, Rosidae near Celastrales according to Cronquist). Unfortunately, palynology does not yet provide a clear-cut answer to either problem. In the Lecythidaceae, a partial series can be seen from tricolpate (tricolporate with lolongate ora ?) to the syncolpate *Planchonia*-type, with specialized grooves at the colpus margins and thickenings at the poles (Muller, 1972, 1973). The syncolpate condition might suggest connections with the Myrtales, though no really close analogs exist there. Similar grains also occur in the thealian family Caryocaraceae (Barth, 1966), but in either case the similarities must be at best parallelisms rather than true homologies, since the syncolpate trend occurs *within* the Lecythidaceae (cf. Muller, 1972, 1973). Palynology helps confirm the relationship postulated by Takhtajan between the Euphorbiales and Thymeleaceae, since the "crotonoid" or "stellate" sculpture pattern, with supratactal triangular and oblong projections arranged in a reticulum, is largely restricted to certain Thymeleaceae, Buxaceae, and Euphorbiaceae (Arkhangel'skiy, 1966a, 1966b). Again, this must be an example of parallelism, since other (presumably more primitive) members of both orders are reticulate and tricolporate; it is these that must be studied in more detail for indications of dilleniid versus rosid affinities.



*Asteridae*.—In keeping with their position as the most advanced subclass in the Takhtajan and Cronquist systems, the Asteridae show a broad spectrum of divergently specialized pollen types. Nevertheless, a few members of the putatively more primitive orders (Caprifoliaceae, *Adoxa*, Loasaceae, Hydrophyllaceae, Buddlejaceae) have relatively small, psilate to finely reticulate tricolporoidate pollen of the type considered above to be primitive in both the Dilleniidae and Rosidae. On the other hand, the tricolpate condition in some Labiatae, Scrophulariaceae, etc., like many other cases of small size (e.g., *Myosotis* in the Boraginaceae), is more easily explained in terms of the Takhtajan and Cronquist systems as a secondary specialization. In the case of the Labiatae, tricolporate pollen is found in the relatively primitive subfamily Ajugoideae and in the related but generally more primitive family Verbenaceae.

A more detailed survey would be required to determine whether the Asteridae are heterogeneous (as believed by Thorne, 1968). However, the “rosid” characters cited above are common enough to suggest that at least some of the Asteridae are rosid rather than dilleniid derivatives. The tendencies for oblate-triangular and sometimes syncolpate grains, which are most striking in the Myrtales, are also common in the Polemoniales (e.g., Boraginaceae, Lennoaceae, Hoplestigmataceae, and especially Hydrophyllaceae, some of which even have pseudocolpi alternating with the colporate apertures, as in Combretaceae), some Gentianales (Menyanthaceae), Lamiales (Verbenaceae), and Scrophulariales (Scrophulariaceae, Solanaceae, Acanthaceae). Striate sculpture may be seen in the Gentianaceae, Menyanthaceae, Polemoniaceae, and especially the Scrophulariales (Solanaceae, Nolanaceae, and Scrophulariaceae).

The Acanthaceae are one of the best examples of a family where the diversity of pollen morphological types was recognized as of systematic importance well before the modern “explosion” of palynological research (e.g., Lindau, 1895). Besides presumably primitive tricolporate grains, this family shows trends for multiplication and shortening of apertures, the origin of tri- and polyporate grains by “fading” in place (rather than shortening) of colpi (a trend also inferred in the Rubiaceae: cf. Erdtman, 1952), and diporate, syncolpate, and even spiraperturate grains.

A few of the more striking asterid specializations may be mentioned. Not only are polyrugate and polyforate grains common (e.g., Martyniaceae, Convolvulaceae, Plantaginaceae), but the trend to numerous equatorial apertures (polycolpate and polycolporate) is more widespread in the Asteridae than in other subclasses, especially in the Scrophulariales and Lamiales (apparently all Pedaliaceae, and many Scrophulariaceae, Bignoniaceae, Lentibulariaceae, Acanthaceae, Verbenaceae, and Labiatae), and also in Polemoniaceae, Rubiaceae, Campanulaceae, and Stylidiaceae. On the other hand, a few Gentianaceae (*Leiphaimos*) show what may be a unique return to the uniaperturate (monoporate) condition, apparently associated with reduction in size in a basically triporate group. The Apocynaceae and Asclepiadaceae have already been cited as showing a trend analogous to that in the Orchidaceae from single grains to tetrads and pollinia. Finally, just as in their inflorescence morphology, the Compositae show a new level of complexity in their exine structure,



with what is considered a second tectum developed within the first in all but the most primitive members, and the elaboration of echinate and (in the Liguliflorae) complex fenestrate sculpture patterns (cf. Wodehouse, 1935, and Skvarla & Turner, 1966, for discussions of the contributions of light and transmission electron microscopy, respectively, to phylogeny of the Compositae).

#### PALYNOLOGICAL TECHNIQUE

Pollen being the size it is, palynology is totally dependent upon use of various types of microscopes. Three major instruments (light, scanning electron, and transmission electron microscopes) are currently available for the study of pollen morphology.

The original and still basic method of studying pollen grains is with the light microscope (photomicroscopy). Palynological material is normally first subjected to an acid treatment or acetolysis (Erdtman, 1960) and then the acetolyzed pollen grains are mounted on permanent slides. Acetolysis performs two main functions: (1) it removes the pollen protoplast, a part of the pollen wall, viz., the intine, and material that may cover the pollen surface such as oil droplets and protein, i.e., pollenkitt and tryphine, and (2) it causes the outer pollen wall layer (exine) to turn from its normal light yellowish-green to a darker amber color. Both of these changes result in the production of greater pollen contrast and permit more detailed study of pollen grains than is possible with non-acetolyzed material. Walker (1971b, 1971d) has modified Erdtman's standard acetolysis method with two features in mind, namely, (1) introduction of a less drastic means of preparing pollen than boiling, which frequently causes a number of grains to be damaged, and (2) development of a method of acetolysis that can handle a large number of individual pollen samples rapidly. In this modified acetolysis treatment pollen is placed in corked centrifuge tubes with standard acetolysis fluid (9 parts acetic anhydride to 1 part concentrated sulfuric acid) in an oven overnight at 50–60°C. The material is then washed once with glacial acetic acid and three times with water. Acetolyzed pollen is then mounted in glycerine jelly and the slides ringed with an air-drying, phenolic varnish in order to make them permanent. The use of disposable Pasteur pipettes was found extremely helpful in transferring a mixture of pollen and glycerine jelly evenly to slides, especially when the available material is scanty. Taxa with reduced exine (such as Lauraceae, Musaceae, etc.) are subjected to KOH-treatment instead of acetolysis. Again, a corked centrifuge tube containing pollen material and varying concentrations of KOH (up to 1 N) is placed in an oven overnight at 50–60°C. The material is then washed in water 3–4 times, stained in basic fuchsin, toluidine blue, and/or alcian blue, and mounted in glycerine jelly.

Whole pollen mounts prepared by these techniques may be studied and photographed in the light microscope at the level of whole grain topography (to determine aperture type for example) and at highest magnification using various focal planes (i.e., LO-analysis) to analyze exine structure and sculpturing (cf. Erdtman, 1966). One may also photograph optical sections of the exine, especially as seen in median optical view. Thin-sections of the exine may also be prepared



for study in the light microscope using paraffin-embedded material and an ordinary rotary microtome (Tseng, 1971).

Pollen samples examined in the scanning electron microscope (SEM) should be subjected initially to acetolysis treatment (Hanks & Fairbrothers, 1970), then transferred from water to double adhesive tape and allowed to dry. Samples may be carbon-coated before coating with a heavy-metal such as gold-palladium prior to their placement within the microscope. The scanning electron microscope greatly complements light microscope studies. The main advantages of the SEM are: (1) great range of magnification, (2) relative ease with which specimens can be prepared for study, (3) considerable depth of focus, and (4) ability to show the pollen surface (sculptural elements) independent of underlying structural components. The last feature is especially important, since the SEM often aids in the interpretation of confusing or ambiguous LO-analyses seen in the light microscope (Walker, 1971d). Also, one may deliberately break pollen grains and study them with the SEM in order to acquire a three-dimensional view of the internal wall structure (cf. Cerceau-Larrival & Roland-Heydacker, 1972).

The transmission electron microscope (TEM) is vital for high resolution micrographs necessary for complete understanding of the pollen wall. The main advantage offered by the transmission electron microscope, besides higher magnification than the light microscope, is the ability to delimit and resolve ektexine-endexine and demonstrate the presence or absence of a foot-layer. Also, measurements of the different wall layers may be carried out much more accurately with transmission electronmicrographs in the case of small grains with thin exines. In some cases both cross and tangential sections are necessary to elucidate the nature of the pollen wall.

#### MAJOR PALYNOLOGICAL REFERENCE WORKS

Mention must be made first of a number of journals which are devoted largely to papers concerned with comparative pollen morphology. The two leading journals in this area are *Grana* (formerly *Grana Palynologica*), which was started by Gunnar Erdtman, and *Pollen et Spores*, which is edited by M. Van Campo. Lately, a series of palynological monographs, the *World Pollen and Spore Flora*, edited by S. Nilsson, have appeared as supplements to *Grana*. A third journal which frequently contains systematic palynological papers, *Review of Palaeobotany and Palynology*, was started more recently. Other pollen journals include the *Journal of Palynology*, published in Lucknow, India, and the *Japanese Journal of Palynology* (published in Japanese).

Palynology is fortunate in having a number of excellent bibliographies, the most comprehensive being the bibliographic supplement published by M. Van Campo each year in the journal *Pollen et Spores*. References published before Mme. Van Campo's bibliographic supplements were started may be found in the earlier palynological bibliographies published over many years by Gunnar Erdtman (cf. Erdtman, 1966, for references). Two other important pollen bibliographies have been published recently. The first of these, "Bibliography of Actuopalynology, 1671-1966," which was published in the journal *Review of Palaeobotany and Palynology*, Vol. 12(1-3), 1971, lists palynological papers by families, while



the second, "Bibliographic Index to the Pollen Morphology of Angiosperms" (Thanikaimoni, 1972), lists each reference by genus.

Books, articles, and reviews which are concerned largely with pollen terminology and/or comparative pollen morphology of angiosperms include publications by Erdtman (1943, 1952, 1963, 1964, 1966, 1969), Faegri & Iversen (1964), Felix (1961), Kapp (1969), Kremp (1965), Reitsma (1970a), Tschudy & Scott (1969), and Wodehouse (1935). Special mention must be made of Erdtman's (1952, 1966) monumental work, *Pollen Morphology and Plant Taxonomy. Angiosperms*, which summarizes what was known about the pollen morphology of every family of angiosperms up to about 1950.

Systematic palynological papers dealing with individual groups of flowering plants have been rapidly increasing every year. The following are just a few examples of angiosperm families which have been the subject of palynological studies since publication of Erdtman's book in 1952: Magnoliaceae (Canright, 1953; Agababian, 1972; Praglowski, 1974), Annonaceae (Walker, 1971b, 1971c, 1972b), Canellaceae (Wilson, 1964), Menispermaceae (Thanikaimoni, 1968), Phytolaccaceae (Nowicke, 1968), Gyrostemonaceae (Priyanto, 1970a), Bataceae (Priyanto, 1970b), Juglandaceae (Whitehead, 1965), Dilleniaceae (Dickison, 1967), Ochnaceae (Muller, 1969a), Sarcolaenaceae (Carlquist, 1964), Caryocaraceae (Barth, 1966), Bombacaceae (Fuchs, 1967), Flacourtiaceae (Keating, 1973), Passifloraceae (Presting, 1965), Fouquieriaceae (Henrickson, 1967, 1973), Droseraceae (Chanda, 1965), Leguminosae-Mimosoideae (Guinet, 1969; Sorsa, 1969), Haloragaceae (Praglowski, 1970b), Alangiaceae (Reitsma, 1970b), Icacinaceae (Dahl, 1952), Coriariaceae (Praglowski, 1970a), Euphorbiaceae (Punt, 1962; Köhler, 1965), Geraniaceae (Bortenschlager, 1967), Loganiaceae (Punt & Leenhouts, 1967), Gentianaceae (Nilsson, 1967), Menyanthaceae (Nilsson, 1973), Polemoniaceae (Stuchlik, 1967), Lennoaceae (Drugg, 1962), Compositae (Stix, 1960; Skvarla & Larson, 1965; Skvarla & Turner, 1966), Palmae (Thanikaimoni, 1970a; Sowunmi, 1972), Araceae (Thanikaimoni, 1969), Commelinaceae (Rowley, 1959), Rapateaceae (Carlquist, 1961), Centrolepidaceae (Chanda, 1966), Restionaceae (Chanda, 1966), and Flagellariaceae (Chanda, 1966).

#### SUMMARY AND CONCLUSIONS

Palynology, although a relatively recent branch of plant morphology, has already provided a great wealth of phylogenetically useful information, thanks both to the ease of extraction of great numbers of specimens and characters from minute amounts of herbarium material, and to the diversity of evolutionary trends, many of which can be verified directly from the fossil record. In angiosperms, the most important trends at the higher taxonomic levels involve the number, position, and structure of germination apertures (closely connected with the form and symmetry of the whole grain), exine structure and stratification, and in some cases size and sculpture.

With some exceptions, pollen morphology is consistent with the levels of relative advancement and the relationships postulated in the Takhtajan and Cronquist systems. Bilaterally symmetrical "gymnospermous" monosulcate pollen and derivative types (inaperturate, disulculate, etc.) characterize both the



putatively primitive dicotyledonous subclass Magnoliidae (sensu stricto) and the monocotyledons. Within the monocotyledons, the primitive monosulcate type is found in all four subclasses; the most striking specializations (monoporate grains, cryptotetrads, loss of exine, and pollinia) are seen in "higher" Commelinidae and Liliidae (grasses, sedges, Zingiberales, and Orchidales). The six non-magnoliid dicotyledonous subclasses are characterized by radially symmetrical tricolpate and derivative pollen types. Relatively primitive reticulate tricolpate pollen is retained by many Ranunculidae, "lower" Hamamelididae, and Caryophyllidae; the Ranunculidae and Caryophyllidae are united by a distinctive trend from tricolpate to globally symmetrical multiaperturate forms. The Dilleniidae (except Dilleniaceae) and Rosidae are somewhat more advanced in having basically compound-aperturate tricolporate pollen; both show parallel tendencies for increase in size and elaboration of exine structure, while the Rosidae show divergent trends related to oblate-triangular shape. The Asteridae exhibit the greatest array of specialized pollen types, but they retain indications of a rosid ancestry. The most important palynological contradiction of the Takhtajan and Cronquist systems is the fact that the highly specialized, basically triporate "higher" Hamamelididae (Amentiferae) can be more directly related to triangular tricolporate Rosidae than to the tricolpate "lower" Hamamelididae.

## LITERATURE CITED

- AGABABIAN, V. S. 1972. Pollen morphology of the family Magnoliaceae. *Grana* 12: 166–176.
- ARKHANGEL'SKIY, D. B. 1966a. Pyl'tsevy zerna semeystv Thymelaeaceae i Gonystylaceae. *Bot. Zhurn.* (Moscow & Leningrad) 51: 484–494.
- . 1966b. Zvezdchataya skul'ptura ekziny pyl'tsevykh zeren. Znachenie palinologicheskogo analiza dlya stratigrafii i paleofloristiki. "Nauka," Moscow. pp. 22–26.
- BAILEY, I. W. & B. G. L. SWAMY. 1949. The morphology and relationships of *Austrobaileya*. *Jour. Arnold Arbor.* 30: 211–226.
- BARTH, O. M. 1966. Estudos morfológicos dos pólenes em Caryocaraceae. *Rodriguésia* 37: 351–428.
- BLAKE, S. T. 1972. *Idiospermum* (Idiospermaceae), a new genus and family for *Calycanthus australiensis*. *Contr. Queensland Herb.* 12: 1–37.
- BORTENSCHLAGER, S. 1967. Vorläufige Mitteilungen zur Pollenmorphologie in der Familie der Geraniaceen und ihre systematische Bedeutung. *Grana Palynol.* 7: 400–468.
- CANRIGHT, J. E. 1953. The comparative morphology and relationships of the Magnoliaceae. II. Significance of the pollen. *Phytomorphology* 3: 355–365.
- CARLQUIST, S. 1961. Pollen morphology of Rapateaceae. *Aliso* 5: 39–66.
- . 1964. Pollen morphology and evolution of Sarcolaenaceae (Chlaenaceae). *Brittonia* 16: 231–254.
- CERCEAU-LARRIVAL, M.-T. & F. ROLAND-HEYDACKER. 1972. Ultrastructure du pollen de *Daucus carota* L. en microscopies à balayage et à transmission. *Compt. Rend. Hebd. Séances Acad. Sci., sér. D*, 275: 2331–2333.
- CHALONER, W. G. 1970. The evolution of miospore polarity. *Geoscience & Man* 1: 47–56.
- CHANDA, S. 1965. The pollen morphology of Droseraceae with special reference to taxonomy. *Pollen & Spores* 7: 509–528.
- . 1966. On the pollen morphology of the Centrolepidaceae, Restionaceae and Flagellariaceae, with special reference to taxonomy. *Grana Palynol.* 6: 355–415.
- CRANWELL, L. M. 1953. New Zealand pollen studies. The monocotyledons. *Bull. Auckland Inst. Museum* 3: 1–91.
- CRONQUIST, A. 1968. *The Evolution and Classification of Flowering Plants*. Houghton Mifflin Co., Boston.
- DAHL, A. O. 1952. The comparative morphology of the Icacinaceae, VI. The pollen. *Jour. Arnold Arbor.* 33: 252–295.
- DICKISON, W. C. 1967. Comparative morphological studies in Dilleniaceae, II. The pollen. *Jour. Arnold Arbor.* 48: 231–240.



- DOYLE, J. A. 1969. Cretaceous angiosperm pollen of the Atlantic Coastal Plain and its evolutionary significance. *Jour. Arnold Arbor.* 50: 1-35.
- . 1973. Fossil evidence on early evolution of the monocotyledons. *Quart. Rev. Biol.* 48: 399-413.
- DRUGG, W. S. 1962. Pollen morphology of the Lennoaceae. *Amer. Jour. Bot.* 49: 1027-1032.
- DUNBAR, A. 1973. Pollen development in the *Eleocharis palustris* group (Cyperaceae). I. Ultrastructure and ontogeny. *Bot. Not.* 126: 197-254.
- ERDTMAN, G. 1943. An Introduction to Pollen Analysis. Chronica Botanica Co., Waltham, Massachusetts.
- . 1945a. Pollen morphology and plant taxonomy. III. *Morina* L. with an addition on pollen morphological terminology. *Svensk Bot. Tidskr.* 39: 187-191.
- . 1945b. Pollen morphology and plant taxonomy. V. On the occurrence of tetrads and dyads. *Svensk Bot. Tidskr.* 39: 286-297.
- . 1952. Pollen Morphology and Plant Taxonomy. Angiosperms. Almquist & Wiksell, Stockholm.
- . 1960. The acetolysis method—a revised description. *Svensk Bot. Tidskr.* 54: 561-564.
- . 1963. Palynology. In R. D. Preston (editor), *Advances in Botanical Research*. Vol. 1: 149-208. Academic Press, London.
- . 1964. Palynology. In W. B. Turrill (editor), *Vistas in Botany*. Vol. 4: 23-54. Macmillan Co., New York.
- . 1966. Pollen Morphology and Plant Taxonomy. Angiosperms. Corrected reprint of the edition of 1952 with a new addendum. Hafner Publ. Co., New York.
- . 1967. On the pollen morphology of *Trigonobalanus* (Fagaceae). *Bot. Not.* 120: 324-333.
- . 1969. Handbook of Palynology. Hafner Publ. Co., New York.
- & H. STRAKA. 1961. Cormophyte spore classification—an outline based on the apertures (tremata). *Förh. Geol. Fören. Stockholm* 83: 65-78.
- & VISHNU-MITRE. 1956. On terminology in pollen and spore morphology. *Palaeobotanist* 5: 109-111.
- FAEGRI, K. 1956. Recent trends in palynology. *Bot. Rev. (Lancaster)* 22: 639-664.
- & J. IVERSEN. 1964. Textbook of Pollen Analysis. Ed. 2, revised. Hafner Publ. Co., New York.
- FELIX, C. J. 1961. An introduction to palynology. Pp. 436-462, in H. N. Andrews, Jr., *Studies in Paleobotany*. John Wiley & Sons, Inc., New York.
- FISCHER, H. 1890. Beiträge zur vergleichenden Morphologie der Pollenkörner. Thesis, Breslau.
- FUCHS, H. P. 1967. Pollen morphology of the family Bombacaceae. *Rev. Palaeobot. Palynol.* 3: 119-132.
- GÓCZÁN, F., J. J. GROOT, W. KRUTZSCH & B. PACLTOVA. 1967. Die Gattungen des "Stemma Normapolles Pflug 1953b" (Angiospermae). *Paläontol. Abh., Abt. B, Paläobot.* 2: 429-539.
- GUINET, P. 1966. Les caractères du pollen dans le genre *Leucaena* (Mimosaceae). *Pollen & Spores* 8: 37-48.
- . 1969. Les Mimosacées—étude de palynologie fondamentale, corrélations, évolution. *Inst. Franç. Pondichéry, Trav. Sect. Sci. Techn.* IX: 1-293 pp., 20 pls.
- HANKS, S. & D. E. FAIRBROTHERS. 1970. Effects of preparation technique on pollen prepared for SEM observations. *Taxon* 19: 879-886.
- HENRICKSON, J. 1967. Pollen morphology of the Fouquieriaceae. *Aliso* 6: 137-160.
- . 1973. Fouquieriaceae DC. *World Pollen & Spore Flora* 1: 1-12.
- HUTCHINSON, J. 1964. The Genera of Flowering Plants. Vol. 1. Dicotyledons. Oxford Univ. Press, London.
- KAPP, R. O. 1969. How to Know Pollen and Spores. Wm. C. Brown Co., Dubuque, Iowa.
- KEATING, R. C. 1973. Pollen morphology and relationships of the Flacourtiaceae. *Ann. Missouri Bot. Gard.* 60: 273-305.
- KENG, H. 1962. Comparative morphological studies in Theaceae. *Univ. Calif. Publ. Bot.* 33: 269-384.
- KÖHLER, E. 1965. Die Pollenmorphologie der biovulaten Euphorbiaceae und ihre Bedeutung für die Taxonomie. *Grana Palynol.* 6: 26-120.
- KREMP, G. O. W. 1965. Morphologic Encyclopedia of Palynology. Univ. of Arizona Press, Tucson.
- KUPRIANOVA, L. A. 1948. Morfologiya pyl'tsy odnodol'nykh rasteniy. *Trudy Bot. Inst. Akad. Nauk. SSSR, Ser. 1, Fl. Sist. Vyss. Rast.* 7: 163-262.



- . 1967. Apertures of pollen grains and their evolution in angiosperms. *Rev. Palaeobot. Palynol.* 3: 73–80.
- . 1969. On the evolutionary levels in the morphology of pollen grains and spores. *Pollen & Spores* 11: 333–351.
- LARSON, D. A. 1964. Further electron microscopic studies of exine structure and stratification. *Grana Palynol.* 5: 265–276.
- , J. J. SKVARLA & C. W. LEWIS, JR. 1962. An electron microscope study of exine stratification and fine structure. *Pollen & Spores* 4: 233–246.
- LEFFINGWELL, H. A., D. A. LARSON & M. J. VALENCIA. 1970. A study of the fossil pollen *Wodehouseia spinata*. I. Ultrastructure and comparisons to selected modern taxa. II. Optical microscopic recognition of foot layers in differentially stained fossil pollen and their significance. *Bull. Canad. Petrol. Geol.* 18: 238–262.
- LINDAU, G. 1895. Acanthaceae. In A. Engler & K. Prantl (editors), *Die natürlichen Pflanzenfamilien* IV, 3b: 274–354.
- MANTEN, A. A. 1970. Ultra-violet and electron microscopy and their application in palynology. *Rev. Palaeobot. Palynol.* 10: 5–37.
- MULLER, J. 1969a. Pollen-morphological notes on Ochnaceae. *Rev. Palaeobot. Palynol.* 9: 149–173.
- . 1969b. A palynological study of the genus *Sonneratia* (Sonneratiaceae). *Pollen & Spores* 11: 223–298.
- . 1970. Palynological evidence on early differentiation of angiosperms. *Biol. Rev. Cambridge Philos. Soc.* 45: 417–450.
- . 1972. Pollen morphological evidence for subdivision and affinities of Lecythidaceae. *Blumea* 20: 350–355.
- . 1973. Pollen morphology of *Barringtonia calyptrocalyx* K. Sch. (Lecythidaceae). *Grana* 13: 29–44.
- NILSSON, S. 1967. Pollen morphological studies in the Gentianaceae-Gentianinae. *Grana Palynol.* 7: 46–145.
- . 1973. Menyanthaceae Dum. *World Pollen & Spore Flora* 2: 1–19. [Taxonomy by R. Ornduff.]
- NOWICKE, J. W. 1968. Palynotaxonomic study of the Phytolaccaceae. *Ann. Missouri Bot. Gard.* 55: 294–364.
- PAYNE, W. W. 1972. Observations of harmomegathy in pollen of Anthophyta. *Grana* 12: 93–98.
- PRAGLOWSKI, J. 1970a. Coriariaceae. *World Pollen Flora* 1: 15–31.
- . 1970b. The pollen morphology of the Haloragaceae with reference to taxonomy. *Grana* 10: 159–239.
- . 1974. Magnoliaceae Juss. *World Pollen & Spore Flora* 3: 1–45. [Taxonomy by J. E. Dandy.]
- PRESTING, D. 1965. Zur Morphologie der Pollenkörner der Passifloraceen. *Pollen & Spores* 7: 193–247.
- PRIJANTO, B. 1970a. Gyrostemonaceae. *World Pollen Flora* 2: 1–13.
- . 1970b. Batidaceae. *World Pollen Flora* 3: 1–11.
- PUNT, W. 1962. Pollen morphology of the Euphorbiaceae with special reference to taxonomy. *Wentia* 7: 1–116.
- & P. W. LEENHOUTS. 1967. Pollen morphology and taxonomy in the Loganiaceae. *Grana Palynol.* 7: 469–516.
- REITSMA, T. 1970a. Suggestions towards unification of descriptive terminology of angiosperm pollen grains. *Rev. Palaeobot. Palynol.* 10: 39–60.
- . 1970b. Pollen morphology of the Alangiaceae. *Rev. Palaeobot. Palynol.* 10: 249–332.
- ROLAND, F. 1971. Données évolutives résultant de l'étude ultrastructurale des apertures de pollens appartenant au groupe Ranales Centrospermales. *Rev. Gén. Bot.* 78: 329–338.
- ROWLEY, J. R. 1959. The fine structure of the pollen wall in the Commelinaceae. *Grana Palynol.* 2: 3–31.
- & A. O. DAHL. 1962. The aperture of the pollen grain in *Commelinantia*. *Pollen & Spores* 4: 221–232.
- SHAW, G. 1971. The chemistry of sporopollenin. Pp. 305–348, in J. Brooks, P. R. Grant, M. Muir, P. van Gijzel & G. Shaw (editors), *Sporopollenin*. Academic Press, London.
- SKVARLA, J. J. & D. A. LARSON. 1965. An electron microscopic study of pollen morphology in the Compositae with special reference to the Ambrosiinae. *Grana Palynol.* 6: 210–269.



- & J. R. ROWLEY. 1970. The pollen wall of *Canna* and its similarity to the germinal apertures of other pollen. *Amer. Jour. Bot.* 57: 519–529.
- & B. L. TURNER. 1966. Systematic implications from electron microscopic studies of Compositae pollen—a review. *Ann. Missouri Bot. Gard.* 53: 220–256.
- SORSA, P. 1969. Pollen morphological studies on the Mimosaceae. *Ann. Bot. Fenn.* 6: 1–34.
- SOWUNMI, M. A. 1968. Pollen morphology in the Palmae, with special reference to trends in aperture development. *Rev. Palaeobot. Palynol.* 7: 45–53.
- . 1972. Pollen morphology of the Palmae and its bearing on taxonomy. *Rev. Palaeobot. Palynol.* 13: 1–80.
- STIX, E. 1960. Pollenmorphologische Untersuchungen an Compositen. *Grana Palynol.* 2(2): 41–104, 21 pls.
- STRAKA, H. 1963. Über die mögliche phylogenetische Bedeutung der Pollenmorphologie der madagassischen *Bubbia perrieri* R. Cap. (Winteraceae). *Grana Palynol.* 4: 355–360.
- STUCHLIK, L. 1967. Pollen morphology in the Polemoniaceae. *Grana Palynol.* 7: 146–240.
- SWAMY, B. G. L. 1949. Further contributions to the morphology of the Degeneriaceae. *Jour. Arnold Arbor.* 30: 10–38.
- TAKHTAJAN, A. L. 1959. *Die Evolution der Angiospermen*. Gustav Fischer Verlag, Jena.
- . 1966. *Sistema i Filogeniya Tsvetkovykh rastenii*. Izdatel'stvo "Nauka", Moscow.
- . 1969. *Flowering Plants: Origin and Dispersal*. Transl. by C. Jeffrey. Smithsonian Inst. Press, Washington, D.C.
- THANIKAIMONI, G. 1968. Morphologie des pollens des Ménispermacées. *Inst. Franç. Pondichéry, Trav. Sect. Sci. Techn.* V(4): 1–56, 16 pls.
- . 1969. Esquisse palynologique des Aracées. *Inst. Franç. Pondichéry, Trav. Sect. Sci. Techn.* V(5): 1–31, 20 pls.
- . 1970a. Les palmiers: palynologie et systématique. *Inst. Franç. Pondichéry, Trav. Sect. Sci. Techn.* XI: 1–286, 22 pls.
- . 1970b. Pollen morphology, classification and phylogeny of Palmae. *Adansonia*, n.s. 10: 347–365.
- . 1972. Index bibliographique sur la morphologie des pollens d'angiospermes. *Inst. Franç. Pondichéry, Trav. Sect. Sci. Techn.* XII(1): 1–337.
- THORNE, R. F. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. *Aliso* 6(4): 57–66.
- TSCHUDY, R. H. & R. A. SCOTT (editors). 1969. *Aspects of Palynology*. Wiley-Interscience, New York.
- TSENG, C. C. 1971. Light and scanning electron microscopic studies on pollen of *Tetraplasandra* (Araliaceae) and relatives. *Amer. Jour. Bot.* 58: 505–516.
- VAN CAMPO, M. 1946. Observations sur l'emploi des grains de pollen en phylogénie. *Bull. Soc. Hist. Nat. Toulouse* 81(12): 1–4.
- . 1966. Pollen et phylogénie. Les bréviaxes. *Pollen & Spores* 8: 57–73.
- . 1967. Pollen et classification. *Rev. Palaeobot. Palynol.* 3: 65–71.
- . 1971. Précisions nouvelles sur les structures comparées des pollens de Gymnospermes et d'Angiospermes. *Compt. Rend. Hebd. Séances Acad. Sci., sér. D*, 272: 2071–2074.
- & B. LUGARDON. 1973. Structure grenue infratectale de l'ectexine des pollens de quelques Gymnospermes et Angiospermes. *Pollen & Spores* 15: 171–187.
- , F. BRONCKERS & P. GUINET. 1967. Electron microscopy's contribution to the knowledge of the structure of acetolysed pollen grains (a critical essay). *Palynol. Bull. (Lucknow)* 2–3, (supplement): 1–21.
- WALKER, J. W. 1971a. Unique type of angiosperm pollen from the family Annonaceae. *Science* 172: 565–567.
- . 1971b. Pollen morphology, phytogeography, and phylogeny of the Annonaceae. *Contr. Gray Herb.* 202: 1–132.
- . 1971c. Contributions to the pollen morphology and phylogeny of the Annonaceae. I. *Grana* 11: 45–54.
- . 1971d. Elucidation of exine structure and sculpturing in the Annonaceae through combined use of light and scanning electron microscope. *Pollen & Spores* 13: 187–198.
- . 1972a. Chromosome numbers, phylogeny, phytogeography of the Annonaceae and their bearing on the (original) basic chromosome number of angiosperms. *Taxon* 21: 57–65.
- . 1972b. Contributions to the pollen morphology and phylogeny of the Annonaceae. II. *Bot. Jour. Linn. Soc.* 65: 173–178, 7 pls.



- . 1974a. Primitively columellaless pollen: a new concept in the evolutionary morphology of angiosperms. *Amer. Jour. Bot.* 61(5, supplement): 51. [Abstract.]
- . 1974b. Evolution of exine structure in the pollen of primitive angiosperms. *Amer. Jour. Bot.* 61: 891–902.
- . 1974c. Aperture evolution in the pollen of primitive angiosperms. *Amer. Jour. Bot.* 61: 1112–1137.
- . 1975. Comparative pollen morphology and phylogeny of the ranalean complex. In C. B. Beck (editor), *Origin and Early Evolution of Angiosperms*. Columbia Univ. Press, New York. (in press).
- . 1976. Evolutionary significance of the exine in the pollen of primitive angiosperms. In I. K. Ferguson & J. Muller (editors), *The Evolutionary Significance of the Exine*. Academic Press, New York. (Linn. Soc. Symp. Ser. No. 1, in press.)
- & E. S. KEMP. 1972. Preliminary studies of exine stratification in the pollen of primitive angiosperms. *Brittonia* 24: 129–130. [Abstract.]
- & J. J. SKVARLA. 1975. Primitively columellaless pollen: a new concept in the evolutionary morphology of angiosperms. *Science* 187: 445–447.
- WHITEHEAD, D. R. 1965. Pollen morphology in the Juglandaceae, II: Survey of the family. *Jour. Arnold Arbor.* 46: 369–410.
- WILSON, T. K. 1964. Comparative morphology of the Canellaceae. III. Pollen. *Bot. Gaz.* (Crawfordsville), 125: 192–197.
- WITTMANN, G. & D. WALKER. 1965. Towards simplification in sporoderm description. *Pollen & Spores* 7: 443–456.
- WODEHOUSE, R. P. 1935. *Pollen Grains*. McGraw-Hill Book Co., New York. [Facsimile of the 1935 edition, published by Hafner Publishing Co., New York, 1965.]